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No. 1. — *Studies from the Newport Marine Zoölogical Laboratory. Communicated by* Alexander Agassiz.

XX.

On the Development of the Calcareous Plates of Asterias.

By J. Walter Fewkes.

1. General Observations.
2. General Changes in External Form brought about by the Growth of the Calcareous Plates.
3. Development of Individual Plates, Rods, Pedicellariæ, Spines, and Stone Canal.
4. Comparisons with other Asteroidea.
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1. General Observations.

Asterias, the most common genus of Asteroidea at Newport, in its development passes through a brachiolarian stage before it assumes a stellate form. This brachiolaria is one of the most abundant larvæ found in our nets in surface fishing at certain times of the year. Although the development of the brachiolaria from the egg of the starfish has been accurately worked out, and the changes in the external form of the young Asterias, after it begins to assume a stellate form, have been well described by several naturalists, we are still ignorant of the mode and place of formation, and the sequence in the development, of some of the calcareous plates which help to give the stellate form to the young starfish after the absorption of the brachiolaria. We need more information as to how the ambulacral plates form, and when they appear, as compared with the dorsocentral and terminals. We do not know how or when certain plates of the arm appear, and it is desirable to study the character of certain so-called embryonic plates reported to exist on the median line of the actinal side of the arm in the larva.

Before we can arrive at any trustworthy conclusions as to the morphology of the Echinoderms, animals as varied in external form as the Crinoids and Holothurians, it is necessary for us to know the character of the early differences in the calcareous plates, and their sequence and mode of growth in the different groups. These plates are the structures which, more than any others, give the variety in external form to the different members of the Echinodermata. It may be confidently said that we know the general outlines of the growth of the primary plates of a representative Comatulid, Ophiuran, and Holothurian. We know next to nothing of the early formed plates of the Echinoids, and there is no subject which offers more interesting possibilities of discovery than this. Little is known of the mode of growth of certain of the plates of the body and arms in those Asterids which have a nomadic brachiolaria.*

The following paper, therefore, is offered as a contribution to the recorded observations on the growth of the plates in the starfish.

The common species of Asterias found at Newport resembles closely *Asteracanthion berylinus* of A. Agassiz, and has close affinities with *Asterias vulgaris*, Sl., and *A. Forbesii*, Desor.† Although I suppose it to be the same as *berylinus*, there are some peculiarities of coloration ‡ which would lead one to regard them as different. While the species of starfishes found by me at Newport, in the adult condition, have features of both *A. vulgaris* and *A. Forbesii*, it is not possible for me to

* Our knowledge of the growth of the plates which form the mouth parts of the starfish is fragmentary and unsatisfactory.

† The genus Leptasterias is thought to be sufficiently well separated from Asterias by the character of its development to merit a new name, as shown by Prof. Verrill.

‡ The fact that all females of both *Asteracanthion pallidus*, Agass., and *Asteracanthion berylinus*, Agass., have a bluish tint, while the males have a reddish color, according to A. Agassiz, indicates that there is a difference in color in the female starfishes which we studied. The color of the females of the species of starfish which I tried to fertilize was different from those of the species of Asteracanthion used by A. Agassiz in the artificial impregnation of the starfish. Many specimens of female starfishes, which had ripe ova, have a chocolate-brown color, and a bright orange madreporic body. Starfishes of this color were the only ones which cast their eggs, although I had in the aquaria bright red and bluish colored starfishes of all sizes. In A. Agassiz's specimens those with a bluish tint are invariably females, while the reddish brown or reddish are males. I do not know the color of our male Newport Asterias, but several specimens of the reddish brown specimens laid eggs in great numbers on several occasions. Ova nearly mature were also cut out of specimens of this color.

determine of which of these my brachiolariæ are the young. As most of the younger stellate forms were raised from brachiolariæ captured by surface fishing, it is almost impossible to say definitely to which species of Asterias they belong. I was not able to fertilize artificially Asterias, although plenty of ripe ova were repeatedly found. The difficulty seemed to be in all cases in procuring the males.

The following mention of their time of ovulation may be of assistance to those who have in mind a visit to the New England coast for the study of Echinoderm embryology.

1. The eggs of Ophiopholis were fertilized at Eastport, Maine, on July 17th. The young of *A. squamata* were found at Newport, R. I., in July, August, and September.

2. Echinarachnius can be artificially fertilized at Newport in August and September. The probable time of ovulation is the end of August and the first weeks of September. Plutei are abundant in September. A specimen of Arbacia laid eggs at Newport in August. I have found the majority of the plutei of Arbacia in July.

3. Large numbers of Leptasterias with attached young were taken in Massachusetts Bay in April. Multitudes of a red pupa of some Holothurian were collected at Provincetown in April.

4. The pupæ of Synapta are found sporadic at Newport in August and September by surface fishing. The auriculariæ of Synapta are found in July.

The material which has served for the following observations on the starfish young was collected in two ways. The younger forms in some instances were raised from the brachiolariæ, collected by surface fishing with the Müller net. This material includes all stages from the first appearance of the plates, or calcareous skeleton, up to the young starfish with three pairs of ambulacral rafters. The remaining specimens, from the young Asterias with three pairs of ambulacrals into the oldest stages figured, were found on the under side of stones near low-tide mark. The large stones near the outer landing-place at the Laboratory were turned over, and the young starfishes were found clinging to them. This method of collecting involves continued search, as Asterias is not common in the immediate neighborhood of the Laboratory.

The method by which the preparations of starfishes described in this paper were made is as follows. The young starfishes were killed in alcohol (35%). They were then rapidly passed through different grades (50%, 70%, 90%) to absolute alcohol. They were then clarified in

clove oil, and mounted in balsam. Those which were stained were carried from 70% alcohol into Grenacher's alcoholic borax-carmine, washed, afterwards placed in from 90% to 100% alcohol, then removed to clove oil and balsam. The preparations mounted without staining show very well the relation of the plates to each other, but it is necessary to use a staining fluid to bring out the tissues of the organs in the immediate vicinity of the calcareous skeleton.

In the study of the plates on the abactinal side of the disk of older specimens, it was necessary to separate the arms from the disk proper. No dissection was resorted to in this separation, for the arms are easily broken from the disk along the suture between the first dorsal plate and the second dorsal radial, leaving the former, as well as the genitals and all intermediate plates between them, on the disk with the dorsocentral. In older stages staining fluid was used, but the best results, as far as the plates are concerned, were obtained in specimens where no artificial staining was resorted to.

The use of chloroform, which gave good results in Amphiura,* was not resorted to in Asterias.

2. General Changes in External Form brought about by the Growth of the Calcareous Plates.

By the growth of the calcifications in the growing Asterias the animal assumes a stellate outline, passing into this form from a spherical or discoid larva. These changes are almost wholly the result of change in form or modification in the arrangement of the plates, but the peripheral appendages, spines, pedicellariæ, and spicules also play an important part in this growth. When the growth of the primary plates begins, the young starfish is not stellate in form, and all the early plates are confined to the body. The elongation of the arms are the most prominent results of the modification in the shape of plates, of addition to those already existing, and of enlargement of the same. In the growth of the arm no marked symmetry in the formation of plates on the actinal and abactinal regions of the arm was noticed. There is also no symmetry observed in the growth of the calcifications in the actinal and abactinal regions of the body.

It is not in the province of this paper to give more of the development of Asterias than is necessary to understand the relation of the

* I tried a few specimens of the young Amphiura with clove oil, and find that this reagent clarifies them better than chloroform.

plates to one another, and to aid in their identifications and homologies. A consideration of the internal organs is a most interesting and necessary chapter in a study of the growth of the stellate form of the starfish, but it is one of which little is written in the present paper. Some idea of the origin of organs in immediate connection with the plates is necessary, however, to understand the homologies of the calcareous formations with which this paper is specially concerned.

The development of the brachiolaria of our common Asterias is well known through the researches of A. Agassiz,* and is not here considered. My account opens with a late stage of the brachiolaria, in which certain calcareous nodules, described in the paper mentioned, have already appeared, and in which the form of a stellate animal is obscurely marked out. It is intended first to follow the general course of growth of these plates collectively, and later in the paper, the development of individual plates will be taken up one after the other.

In the starfish body, as is well known, there are two regions, called the actinal and abactinal, the lower and upper, ventral and dorsal, which may be studied. The primary plates in these two hemisomes differ from the very first in number, arrangement, and distribution. No plate is ever formed in the centre of the actinal hemisome comparable with that in the middle of the abactinal, and it would be a task which the author is not called upon to undertake to compare the ten ambulacrals formed on the lower hemisome with the five terminals and five genitals of the abactinal region of the body.

In the early condition of the plates there is an indication of the disk-like form which the young Asterias has, but it is somewhat masked. If we look at the lower or anal pole of the brachiolaria (Pl. I. fig. 1) laterally, and in such a way that the forming plates are on the side turned to the observer, we can see ten small calcifications, arranged in two U-shaped lines, one within the other. If we so place the brachiolaria that the anal pole is below, or pointing to the lower side of the figure, the madreporic body on the left hand of the observer and the anus of the brachiolaria on his right, we notice the five plates, now in

* On the Embryology of *Asteracanthion berylinus*, Ag., and a Species allied to *A. rubens*, M. T., *Asteracanthion pallidus*, Ag. Proc. Amer. Acad. Arts and Sci., VI., 1863. Also separate, 1863.

Embryology of the Starfish, published in December, 1864, advance Pt. I., Vol. V., Contrib. Nat. Hist. of U. S., of L. Agassiz. — The same, reprinted with descriptions of the hard parts (calcareous skeleton) of several genera and species of Asteroidea, under the title, "North American Starfishes," Mem. Museum Comp. Zoölogy, V., No. 9, 1877.

the form of calcareous spicules, $t^1 - t^5$, of the larger U, beginning with one, t^1, just south of the madreporic opening; followed by a second, t^2, a little east of south of the first; a third, t^3, north of east of the second; a fourth, t^4, east of north of the third; and a fifth, t^5, about due east of the first. With these alternate the rods of the smaller U, the first, g^1, being placed about east of the madreporic opening, the second, g^2, third, g^3, fourth, g^4, and fifth, g^5, alternating respectively with the 1st – 2d, 2d – 3d, 3d – 4th, 4th – 5th, of the larger U. The members of the larger U are the terminals; those of the smaller U the genitals.* Between the first genital and the fifth terminal lies a broader space than between other consecutive plates, which is the open part of the larger U. It is an unclosed region which forms the brachiolarian notch. As the brachiolaria is slowly absorbed, this notch is more and more reduced in extent, until it is almost wholly lost, when by this reduction the two Us become rings forming the abactinal calcareous surface of the young starfish.

If now we rotate the brachiolaria on its axis, through a right angle, so that the madreporic body faces the observer, the anal pole being still below, we have the following perspective of the two Us. It will then be seen that the larger and the smaller Us do not lie in one and the same plane, but that the U formed by the terminals is situated on a greater circle than that of the genitals. This fact explains why it is that the figure formed by the line of the latter is smaller than that of the former. It is as if the U of the terminals was placed on the great circle of a hemisphere, while that of the genitals follows a smaller. The difference in size of the two letters (U) is due to the spherical form of the walls of the stomach of the brachiolaria.

It is somewhat difficult to understand the exact relationship between the dorsal and ventral or abactinal and actinal† surfaces of the young starfishes, and the relation of the plates which form in these two regions. These two surfaces are separated by the stomach of the brachiolaria, and are not at first parallel, but form an acute angle with each other; and if the plane in which the plates of the abactinal hemisome were continued to meet that of the primitive extensions of the water tubes, they would cut each other at a small angle. A. Agassiz described them as two "warped spirals," and if in early stages lines be drawn, connecting the terminal and genital plates, the planes in which they lie will be

* The term "genital" is used to denote the same plates as "basal" by Sladen.

† "Ambulacralen" and "Antiambulacralen Anlagen" of Ludwig (Entwicklungs-geschichte der *Asterina gibbosa*, Forbes).

found not to be parallel with the plane in which a line drawn through the tips of the radial water tubes, or the first-formed ambulacral plates lie. As absorption of the brachiolaria goes on, however, these planes get more and more nearly parallel, so that the two surfaces equidistant from the axis are equidistant from each other at all points.

Each of the five small *culs-de-sac*, *rw*, from the water tube on the ambulacral side of the young starfish forms a radial water tube of the starfish; and if a line be drawn from the tip through its middle to the centre of the mouth, it might be thought to indicate the line of the ray. In the same way, if a line be drawn from each of the notches in the margin of the young starfish (Pl. I. fig. 3) through the centre of the mouth, it might be thought to indicate an interradius of the abactinal side. The radius and interradius thus formed have in the adult a definite relationship to each other. They do not coincide, as they indicate entirely different regions of the young starfish. If such lines be projected in Plate I. fig. 3, it will be seen that there is a very great variation in their relative distances from each other. This difference is in part due to the obliquity of the two planes of actinal and abactinal regions of the starfish.

The first addition, on the abactinal side, to the ten plates which form the two Us of the early stages, is a small calcareous nodule, situated within the smaller U near the fifth genital (Pl. I. fig. 2). This nodule is the beginning of the dorsocentral, *dc*, and in the subsequent growth of the fifth terminal towards the first genital by the absorption of the brachiolaria, and the consequent reduction in size of the brachiolarian notch, it is brought to occupy the centre of the abactinal region of the starfish. The anus of the brachiolaria, which is the blastopore of the gastrula, is situated quite a distance from this plate, and not near it as recorded in Asterina.

The growth of the fifth terminal, t^5, towards the first genital, g^1, which from its vicinity to the madreporic opening is called the madreporic body, is brought about by an absorption of the brachiolaria, and the reduction in width of the notch as stated above. Before the complete closure of the brachiolarian notch takes place, however, the terminals have grown so large that marginal notches corresponding to interradii have formed between them (Pl. I. fig. 2) on the rim of the body, and an approach to the stellate form begins to be visible. The increasing growth of the rods of the forming star adds so much weight to the brachiolaria that it sinks to the bottom of the aquarium in which the animal is confined. The eleven plates of the abactinal region of the

starfish antedate all plates on the actinal surface. With the formation of the eleven plates of the abactinal hemisome, how fares it with the actinal? What plates have been added to this portion of the body?

If we so place the brachiolaria that the side opposite that already described (abactinal) is made to face the observer, it will be seen that the future circular water tube on this side (actinal) has the form of an elongated U-shaped tube, with five blind extensions (*culs-de-sac*, fig. 3, *rw*). If we focus the microscope down to the plates below, which lie on the actinal surface, on the opposite side of the stomach, it will be seen that each of these blind extensions of the tube corresponds roughly with a radius of the starfish. Like the disk, the circular tube has likewise a brachiolarian notch, but it is unclosed as yet. This tube and its extensions are the water-vascular tubes of the future starfish; the unclosed U-shaped portion, the circular tube; the prolongations, or *culs-de-sac*, are the beginnings of the median actinal water vessel * of the starfish rays.

One remarkable fact in regard to the relation of the system of vessels to the abactinal plates may be mentioned. The middle of the region on the periphery of which the circular tube of the actinal vessels lies, or the mouth, does not coincide with and is not opposite to the dorso-central, or the central plate of the abactinal hemisome, but is more nearly opposite the point of origin from the circular vessel of the madreporic tube. This dislocation has been brought about by the fact that the fifth terminal has grown to be much larger than the first terminal. Moreover, the indentation which separates the first terminal from the second, is in early stages quite obscure, for some unknown reason. The same is true of the circular tube which near the fifth terminal, t^5, is well formed, while near the first terminal, t^1, it is as yet unclosed. The first radial median projection is half formed. This condition is due in part to the fact that the plane of the water ring is not yet quite parallel with that of the terminals, as explained above, on the abactinal hemisome. The unequal development would seem to indicate that the fifth terminal is the first to form, and that the first terminal is the latest

* The primary form of the circular bloodvessel of Asterias can be seen in Plate I. fig. 3, *cbr*. It occupies the same position as the homologous structure in Asterina, and skirts the walls of the opening of the œsophagus into the stomach and the primitive water vessel. Extensions or radial vessels extending from this into the arms were not noticed, and the central tube, *cwr*, is as yet not closed in or united at the brachiolarian notch. The early-formed nervous ring lies on this region of the starfish, on the bloodvessel; but its tissue is with difficulty distinguished from that of the bloodvessel upon which it lies.

formed terminal. It would seem to indicate that the madreporic opening was a fixed point of departure, as far as the age of plates is concerned. Unfortunately for this conclusion, it is only conjectural that such is the case, and the terminals seem to arise simultaneously. On the other hand, my observations on Asterias do not agree with Ludwig's on Asterina, that the madreporic plate, or the genital near the madreporic opening, is larger than the others, or has a predominance in size in early stages.*

On each side of the radial water tubes, near the circular tube, in their early condition, are formed the ambulacral oral plates, *am*, which are placed at first in parallel pairs and are ten in number. The progress of the growth of these plates and the addition of new ambulacral rafters will be treated of in a special account of the growth of these plates. It is to be noticed that the oral plates are in parallel pairs at first, like the spoon-shaped plates, and other ambulacrals of Amphiura.

Prominent among the calcareous formations which mark this stage (Pl. I. fig. 3) in the development of the starfish are the abactinal spines, *sp*, which appear first on the terminals, and later on the genitals. Their early appearance introduces a morphological question in the discussion of the homologies of the Echinoderms.

In a disk-shaped starfish (Pl. II. fig. 1) which follows hard on the last, the brachiolaria has been almost wholly absorbed, and the brachiolarian notch is very much diminished in width. The relationship of the madreporic tube and the madreporic opening to the genital plate, g^1, is indicated by an arrangement of the branches of the calcareous spicules on the outer border. There is no true madreporic body or superficial calcification until after the stone canal has begun to form,

* In this way I interpret what Ludwig says (pp. 49, 50), in speaking of the eleven first-formed abactinal plates: "Ist doch eines, welches den übrigen zehn fast immer etwas voraus ist in Bezug auf die Zeit seines ersten Auftretens. . . . Aus diesem Skelettstück wird die Madreporenplatte des Seesternes."

In one or two specimens the predominance in size of the interradial (*pace*, Carpenter) plate near the madreporic opening was thought to exist, but in others no such prominence was noticed. No preparation which was made shows the "madreporic plate" without one or two other genitals, and I have none with this plate without terminals.

As Ludwig has shown in Asterina, all the terminals and other genitals do not appear always simultaneously in Asterias. The dorsocentral is generally belated, and one or two genitals may be developed after the others. The same may also be true of the terminals. (Ludwig, Entwicklungs-geschichte der *Asterina gibbosa*, Forbes, Zeit. f. Wiss. Zool, Vol. XXXVII., 1882.)

but a notch where it is later situated appears in a genital long before the calcification of the stone canal has appeared. The madreporic opening, as shown by Ludwig's figures of Asterina, lies to the left of the first genital.

The stellate form of the starfish is brought about by the growth of the plates of the arms, by which the terminals or first plates to appear in the body are pushed out to the extremity of the rays. Among the most important of these plates, on the abactinal side of the body, are the dorsals, *d*, and the marginals or laterals, *m*. On the actinal side, the ambulacrals, *am*, and the interambulacrals, *ad*, accomplish a similar result. All of these plates follow in their growth a general law, viz. that the new plates are formed between those which have already appeared and the terminals. A somewhat similar law holds in regard to the formation of the plates on the disk between the dorsocentral and the first radial or median dorsal. In the case of the latter plates (dorsals, *d*), however, those nearest the dorsocentral are the last to form. The first radial, *d*, or first dorsal, is therefore a point of departure, on either side of which calcifications appear. On the arms the first formed plates are nearest the first dorsal. In the plates formed in Amphiura, the primary radials, or radialia, have a similar relationship.

In the general development of the water-vascular system, it may be noticed that the extensions, *f*, from the medial water tube, which form the ampullæ, are formed before the ambulacral rafters which ultimately separate them. The feet, *f*, are at first destitute of suckers, and are arranged in two rows (Pl. III. fig. 3) in each arm, one row on each side of the middle line. A terminal tentacle (Pl. III. fig. 4, *tta*) was observed in a young starfish, in which there are but two pairs of lateral feet, and no ambulacral rafters. Even in this early stage the eye spot is well developed on the terminal tentacle, *tta*.

The madreporic tube forms a conspicuous object in early starfish larvæ, and passes by successive change into the madreporic canal of the older specimens. The calcification of the canal was observed in early specimens before the formation of the madreporic sieve, which is found superficially on the abactinal surface of the adult. The cribriform madreporic plate is of comparatively late formation in the growth of the starfish. None of the important primary plates of the young starfish form by a constriction from others previously formed, but each kind of plate originates from its own calcification. Plates which have originated from two centres rarely consolidate, although their connection may be of a very intimate nature.

In all the stages which have been studied no embryonic plate or plates were found which are at one time well formed and later lost by absorption. I have looked for these plates especially along the median actinal line of the arm, but was not able to discover them. The large size of the spines would seem to stamp them as embryonic organs. Certainly the size of the spine on the dorsocentral or on the terminals is relatively much larger than in the adult and older stages. This predominance in magnitude of these appendages does not necessarily mean that they are later lost, but it simply indicates a relationship of Asterias in its youth to spiniferous forms. The later growth, when new spines form, simply brings the spine to lose its relatively great size on account of a corresponding growth of the plate and other spines.

3. Development of Plates, Rods, Pedicellariæ, Spines, and Stone Canal.

The following calcifications are considered in this place: —

Body.

Abactinal hemisome.

1. Dorsocentral (Centrale, *Ludwig*), *dc.*
2. Genitals (Basals, *Sladen*, Interradialia, *Ludwig*), $g^1 - g^5$.
3. Plates on the radial line, dd^1.
4. Abaxial interradials, *gg*, gg^1.
5. Connectives,* *c.*

Actinal hemisome.

1. Ambulacral orals,† *am.*
2. Interambulacrals ‡ (Adambulacrals, *auct.*), $ad - ad^5$.
3. (Odontophores §); First Interbrachials, *auct.*
4. Interbrachials, *auct.*

Arms.

Abactinal.

1. Terminals, $t^1 - t^5$.
2. Dorsals ‖ (Intermediäre, *Ludwig*), $d - d^7$.
3. Marginals (Interambulacrals, *Ludwig*), $m - m^7$.
4. Dorsolateral, *dl.*
5. Connectives, *c.*

* By the connectives the smaller plates connecting the larger are meant.

† I should prefer the term Oral, if the name had not been applied to certain other plates.

‡ It may be as well to retain the old term, especially as they arise between ends of successive ambulacrals.

§ An unfortunate designation. I prefer Interbrachial. First homologized by Ludwig with oral, later (*op. cit.*) with unpaired marginal (Unparige Interambulacral).

‖ The first of the dorsals is homologized with radial of crinoid by Sladen.

Actinal.

1. Ambulacrals, Ambulacral rafters.
2. Interambulacrals (Adambulacrals of late authors).

In addition, the following calcifications, appendages to the above plates, are considered : —

1. Spines.
2. Pedicellariæ.
3. Stone canal.

The last is an internal calcification, which is morphologically distinct from the above, and arises in the walls of the water tube.

It is thought that almost all the larger calcifications of the mature Asterias can be referred to some of the above-mentioned structures. There are, however, spicule-like calcifications, as in the legs, which are not considered in this discussion.

The plates first appear as a small calcareous formation in the midst of cells, which color with reagents more deeply than those of the remaining parts of the body in the immediate vicinity. A common form following the simplest is the extension of arms — commonly three — which impart to the spicule a trifid shape. The extremity of each branch subdivides, and continues division, anastomosing and joining with other bifurcations from other branches. The thickness of the calcification is at first small, being simply that of a spicule-like rod. By the growth and anastomosis of the spicules the plate later assumes the form of an open network. This network, in large plates like the terminals and genitals, is open. In other plates, as the median dorsal, the calcification has from the first the form of a disk in which are small perforations.

The interambulacral plates are never thin, with loose open work, but become compact at the very beginning of their development. It is probable that the open character of the early formed terminals is correlated with the fact that these plates are formed in the brachiolaria. It is questionable whether such slight rods would be strong enough to preserve the shape of the stellate animal if they occupied the position of ambulacrals, laterals, or dorsals, and were formed at the same time. These latter plates are more compact from the beginning, for obvious reasons. When the brachiolaria is absorbed, and the terminal comes to be pushed out in an exposed position, its form and compact calcification is such as successfully to resist any injury which its exposure might bring. It not only is strong enough for its own safety, but it serves as an effectual shield for the newly formed ambulacral, interambulacral, dorsal, and

other plates. It is possible, in this connection, that the large spines of the terminals may also serve as structures for protection of the tip of the ray. Animals small enough to take the young starfish for food might well hesitate before eating an animal bristling with the sharp needles of the rays of the young Asterias. While such an explanation may be probable, it also seems not unreasonable that these enormously large spines point to features of the ancestors of the starfish, and have a morphological significance.

It is likewise to be noted, that in many genera of Asteroidea the primarily formed spines are relatively of great size. This is also true of many Ophiuran genera, as Ophiothrix and Ophiocoma. Among Echinoids, Echinarachnius and several others have large primary spines, and in the former genus, as I have already pointed out, these spines appear very early in the embryonic history. Their existence in these groups would seem to indicate a morphological meaning.

It seems to me a significant fact, however, that while in Ophiothrix the spines of the terminals bear the form of large hooks, as I have noticed in an Ophiothrix from Santa Barbara, Amphiura *in the pouch of its mother* is destitute of terminal primary spines. The spines of the larval Asterias are larger than those of the larval Asterina.

The general character of the above plates are as follows: —

Flat, discoid. — The interradials, connectives, dorsocentral, dorsals, and dorsolaterals are flat, discoid, or cylindrical in shape.

Massive, quadrangular. — The interambulacrals are quadrangular and massive.

Curved, crescentic. — The marginals and genitals are crescentic or curved, or more or less bent out of a plane surface.

Elongated in the plane of first calcification. — The ambulacral rafters are elongated in the plane of the first calcification, and have the form of bars or beams, rather than flat plates.

Elongated at right angles to plane of first calcification. — The spines are elongated in the plane opposite that in which the first calcification occurs.

Cap-shaped. — The terminals are cap-shaped.

Tubular. — The calcification of the stone-canal is tubular and multiple, or originating from several centres.

Double calcification in same organ. — The calcification of the pedicellariæ is double from the first.

The above classification is not intended as a hard and fast division, but only as a means of roughly separating the plates from each other.

The different divisions grade into each other, and in early conditions are not distinguishable.

Dorsocentral. — The dorsocentral plate (*dc*) is one of the earliest to form, and is one of the least modified in its growth, of all the abactinal plates of the body. It is believed to be homologous with the dorsocentral of Amphiura. Especial attention was paid to the time when the dorsocentral forms in Asterias, and the development or stage of growth of the terminals and basals when it first appears. This is believed to be an important fact in comparisons both with Ophiurans and with Echinoids.* The younger the larva is, the greater is the distance of this plate from the plutean anus, or blastopore.†

In the youngest starfish (Pl. I. fig. 2) in which the dorsocentral was observed, there were five terminals, $t^1 - t^5$, and five genitals, $g^1 - g^5$. On the periphery of each of the terminals there were two trifid spicules, *sp*, which later developed into the terminal spines. The stellate form, or the position of the interradii, was mapped out by slight indentations in the rim of the disk between the terminals. The terminals have the form of simply bifurcated and Y-shaped calcareous rods. The position of origin of the dorsocentral is in a small space of the dorsal or abactinal region enclosed by the second, third, fourth, and fifth genitals. It is hemmed in by these plates except at one place, the brachiolarian notch, which is an unclosed interval separating in the present stage the first genital from the fifth terminal.

The dorsocentral originates as a simple calcareous rod, or nodule,

* I have already elsewhere (Bull. Mus. Comp. Zoöl., XIII., No. 4, pp. 122, 123) devoted some space to a discussion of the time of appearance of this plate.

† The dorsocentral of Asterias is never as near the blastopore as in Asterina. This fact is mentioned as its neighborhood in the latter has been used by Carpenter in comparisons of the centrodorsal and dorsocentral. Facts in Asterias do not support the supposition, that, when the dorsocentral first appears in this genus, it is closer to the blastopore than in older stages, as Carpenter says is the case in Asterina. This does not deny that it may not be nearer in Asterina, but it is not in Asterias. In Asterias no anus is formed, but the blastopore, which never opens among the limestone plates, is simply closed after absorption of the brachiolaria. I am inclined to the opinion that the blastopore does not become the permanent anus, but have made no observation on this point except that in my species of Asterias the blastopore (brachiolarian anus) is simply closed, and never migrates around the rim of the young starfish to the abactinal side. A. Agassiz, however, considers that there is a close approximation of the calcareous plates and the anus, and says (*op. cit.*, p. 46) that the "anus undoubtedly discharges at this time through one of the many limestone cells." But later he says, "I am not able to state this positively, never having seen from any point discharges of fecal matter."

which immediately grows into a trifid spicule. As the starfish matures the dorsocentral becomes branched (Pl. I. fig. 3), forming a flat pentagonal plate occupying the central region of the abactinal part of the body of the starfish.

As the starfish grows older, the dorsocentral is found to carry a large, well marked, centrally placed spine (Pl. II. fig. 4); later, two and three other spines of large size form. These spines are relatively to the size of the starfish much larger than those of the adult.

In the oldest larval starfish (Pl. IV. fig. 4) which was studied, the dorsocentral still preserves its pentagonal form, and, on a line passing through the dorsal region of the starfish arm, from its angles arise the radials of the disk. The dorsocentral always preserves its central position even into the adult starfish, and never undergoes any considerable modification in outline or in size, although of course its size relative to that of the starfish is smaller as the starfish matures.

The time of development of the dorsocentral in Amphiura is *after* the primary radials and basals.* As there are at first no plates which can be compared with the radials in Asterias, we can simply say that the dorsocentral is formed in the starfish after the basals; but if we compare the first median dorsal arm-plate of the starfish with the radial of Amphiura, we must say that the dorsocentral originates before the first radial in the starfish. This seems to me an additional argument, although I confess not a strong one, against considering the first median dorsal arm-plate as homologous with the radialia, or primary radial, of Amphiura. Still it would seem that the relative time when plates appear in the Echinoderms is unimportant, as far as a determination of their morphology is concerned. My observations on the time the dorsocentral plate appears, as compared with the ten primary plates of Asterias, support the statements of A. Agassiz on this point.

Terminals. — The terminals, $t^1 - t^5$, are the most conspicuous and largest of all the primary plates in the embryonic life of the starfish. While the starfish is yet in the brachiolarian stage (Pl. I. fig. 1) the terminals appear, and in the oldest form considered they are still prominent. From first to last, then, these plates are important calcifications in the growing Asterias and in the modifications of its form. There are five terminals. These will be designated in the following way. Beginning with the madreporic opening, t^1, and ending near the same body, t^5, passing around the anal pole of the brachiolaria from dorsal to ventral side, they extend through a complete semicircle. The termi-

* Bull. Mus. Comp. Zoöl., XIII., No. 4, p. 121.

nals seem to arise almost simultaneously, although brachiolariæ have been found with two, three, or four terminals. The five terminals are, however, all believed to be formed before the genitals appear. The ring of terminals, beginning with t^1 near the madreporic body, are placed in their U-shaped figure at about equal distances apart, with the exception of t^5 and t^1. The space between these two last is the whole diameter of the stomach of the brachiolaria. This space, which in older stages appears as a notch separating the first genital, g^1, from the fifth terminal, t^5, is the brachiolarian notch. It is the notch which marks the position of the madreporic body, and renders it a point of departure in all morphological comparisons of the different groups of Echinoderms. The notch and madreporic opening are separated by the first genital, g^1.

The stage of the young starfish directly following the one in which the dorsocentral is first seen shows a condition in which the terminals have elongated and extended Y-shaped appendages at their extremities. These extensions have formed a rod perpendicular to the radius connecting the dorsocentral with the margin of the forming starfish. The law of the first growth of the terminal seems to be that they elongate, forming an extension across perpendicular to the radial lines, not parallel with them. The spines of the terminals appear directly after the dorsocentral, while yet the terminals are simple spicular bodies. Notches now begin to deepen in the interradii of the forming starfish on the border of the disk, separating the terminals. The terminals never coalesce with their neighbors. Although the terminals originate in the body of the starfish while yet a swimming brachiolaria, and form the most conspicuous plates in the Asterias before the stellate form is marked out, they are ultimately pushed to the extremities of the rays by the growth of the plates of the arms. The first appearance of the stellate form of the young Asterias results from the enlargement of these plates. The terminals originate on the abactinal side of the body, and grow down on the sides of the water-vascular portion of the extensions from this system. By this growth they enclose the tube above and on two sides, and come to have a cap-shape, an opening being left on the terminal border for the passage of the tentacle. There is no growth downward at the tip of the radii in which they lie, but a groove is left at that point through which later the extremity of the medial vessel extends, and in which point the eye-spot is situated.

The cap-shaped form of the terminals affords ample protection for the immature ambulacrals, *am*, interambulacrals, *ad*, and marginals, *m*, which first form under cover of the sides and dorsal portions of the

terminals. This protection to the delicate forming calcareous plates is afforded in later stages in the growth of the starfish arm, even in specimens an inch or more in diameter. As the starfish grows older, the terminals lose their prominence. The large spines and pedicellariæ which first form on the terminals are specially treated of elsewhere. It may here be said that the spines of the terminals are the first spines to form in the Asterid body. The same sequence and predominance are true likewise of the pedicellariæ.

The general form of a terminal of an older starfish (Pl. III. fig. 3) is such that it completely covers the tip and a part of the dorsal region of the end of the arm. That part which covers the dorsal tip of the arm is thinner than that upon the sides, and the groove through which the end of the radial tube, or the tentacle, passes, is well marked.

Medial Dorsals of the Arms. — A row of plates along the crest of the abaxial region of the arm of the starfish may be called dorsals or medial dorsals. The median dorsal row of plates does not begin until after the formation of three pairs of ambulacrals, and likewise subsequent to the odontophores, mouth plates, genitals, terminals, and dorsocentral. The starfish has begun to have a pentagonal or stellate form before the first of this series develops. The first (*d*) of these plates to form appears in the medial dorsal line of the radius, in the triangular space between two genitals and the adoral edges of the terminals (Pl. IV. fig. 1). It antedates the adambulacrals and the laterals. The new dorsals (Pl. IV. figs. 3, 4) form distally to those which have already appeared.

The question of what plates in Amphiura the first of the dorsal plates corresponds to will be spoken of later. There are no radials formed before the terminals inside the ring of genitals; but in other ways, as far as position goes, the oldest of the series of median dorsal plates of the arm corresponds with the first radial of Amphiura. When the arm of the young starfish is broken from its disk, the line of fracture commonly leaves the first dorsal with the arm, not with the disk. The median row (Pl. IV. fig. 4) of dorsal plates form in a continuous series on the middle line of the dorsal (abactinal) region of the arm. The newest formed plates, d^6, d^7, are those outside the plates already formed. They begin as a simple branched calcareous spicule, and broaden into a flat plate. Each median plate bears at first a single spine. The second median dorsal plate forms after the first pair of marginals and the first pair of interambulacrals. The oldest radial has a quadrate form; the others, when well developed, are triangular, with re-entrant angles, by which are developed lateral rings and a median adaxial extension.

The median row of plates is well marked, even into stages of the starfish of some size, and each plate bears at first a single spine.*

Lateral Dorsal Plates. — The larger members of the network of plates which connect the median dorsals with the marginals may be known as the lateral dorsal plates. They were first detected in a young starfish in which were four median dorsal plates; and the first pair to appear is situated on one side of the third median dorsal. In a specimen older than the last these plates were found on the second, third, and fourth median dorsal plates. It will thus be seen that the first lateral dorsal to form is not the pair which belongs to the first, but to the third, median dorsal.

The lateral dorsals (*dl*) are semicircular or circular plates, with their longer axes at right angles to the line of the radius. They are in young stages destitute of spines. There seems to be little regularity in the formation of additional lateral dorsals, and in older conditions they form a dædalus of plates very difficult to trace. They are intimately connected by smaller calcifications, which will be spoken of as the connectives.

Genitals.† — The genitals (g^1–g^5) are the first interradial plates to form. These plates are among the earliest plates of the starfish brachiolaria, and in early stages in the growth of the body they are very conspicuous. They probably originate after the terminals, and appear at first as small calcareous nodules, alternating with the terminals. All of the genitals, in young stages, are smaller than the terminals. The fact that they originate after the terminals is not an unimportant one, as it shows that in this particular the starfish resembles Amphiura. Moreover, it has been stated that one (g^1) of the genitals — namely, that near the madreporic body — arises before the terminals. I find this statement, as well as another that the size of the "basal" (genital) near the madreporic opening is larger than the remainder, and preserves its preponderance in size in all younger stages of the growth of the starfish, not to hold in the specimens of Asterias which were examined.

The genitals when first formed are simple nodules, which later form branched spicules, as shown in Plate I. fig. 1. They lie in the interval of the interradii between the terminals, while their centre of calcification always begins in an interradius.

* The median row of dorsals and their spines correspond with the "median line of spines supported by a long narrow limestone plate extending from the basal plate almost to the terminal radial," mentioned by A. Agassiz (p. 51, *op. cit.*).

† The same plates as those called in several late writings the basals, from their supposed homology with the basals of Crinoids.

The genitals never leave, or are pushed from, the body of the starfish, but as the complexity of their reticulation increases they fill almost the whole space of the interradius between the radially situated terminals.

The genital which occupies the interradius in which the brachiolarian notch lies, differs from the others in possessing an indentation on one side which is perforated by the madreporic opening. This failure of calcification is brought about by the growth of spicular extensions from the edge of the genital which lies contiguous to the madreporic opening, but is marked in no other conspicuous manner.

It will be seen, on a comparison of my description of the way the actinal plates of the starfish form with that given by A. Agassiz,* that there is a difference in our accounts of the growth of these structures. It would seem doubtful that so great a difference could be the result of our studying different species or genera. According to Agassiz,* the large clusters of calcareous deposits which I suppose to be the terminals "unite along the edge of the rays, forming a continuous network," and they are figured with such a union in Plate VI. fig. 10.* It does not appear that he considers those plates which lie in the angle of the rays as joining with the ray plates, or terminals, although remaining distinct from each other; for, later, he says that the limestone deposits in the angles of the rays do not unite laterally.

It would seem exceptional to suppose that the terminals do join or unite at their edges, and that the first interradial plates, or genitals, unite with them. Such a consolidation would prevent, for a time at least, any subsequent growth of the arms, unless we suppose a resorption to take place. The plates simply interdigitate with each other in Asterias, and there is no union, temporary or permanent, between terminals and interradially situated plates or genitals. It is extremely difficult to distinguish the boundaries of the terminals and genitals in live specimens, and it was only by the use of alcohol and some clarifying reagent that I was able to make out the separation of the two.

Interambulacral Plates. — The interambulacral plates, *ad*, originate after the corresponding ambulacral rafters, as separate calcifications between the lateral † ends of successive ambulacrals. In their early

* "North American Starfishes," pp. 46, 48. In my references to A. Agassiz's observations on the embryology of the starfish I have quoted from this paper (Mus. Comp. Zoöl., Vol. VI.). This reprint contains valuable references to the work of other observers made since the paper was first published.

† Most distantly removed from the median radius.

condition they are protected by the cap formed by the sides and dorsal region of the terminals, and, as the terminals are pushed out by growth of dorsals and marginals, new interambulacrals continually form under the shelter of the terminal. The law of development of ambulacrals and marginals, in the arm holds in the interambulacrals. The oldest formed are those nearest the mouth; the youngest are the nearest to the terminals. The beginnings of at least three pairs of ambulacrals are formed before the first true interambulacral appears. The marginals antedate the interambulacrals.

There is little variety in the progress of the growth of the interambulacrals, from the time they first appear as small calcareous nodules (Pl. III. fig. 2) until they form the compact blocks of older stages in the growth. They differ from most of the other plates of the starfish in their massive growth, and they never have the flat perforated plate form of the dorsals or genitals. As they mature, they fit closely together, forming square blocks with re-entering angles, and are closely articulated. They also carry a single long spine in early stages.

In younger forms of the starfish, before the ambulacrals have become so crowded that there are four rows of feet, the interambulacrals alternate with the ambulacrals. At that time the number of interambulacrals is the same as that of the ambulacrals, with the exception, however, of the newly forming ambulacrals at the extremity of the ray. In all young starfishes the single row of interambulacrals stands out clear and distinct from the other plates, while their number always has a constant relation to that of the ambulacral rafters.

Marginal Plates. — Large and important plates of the arms, originating early in the development of the larva, may be known as the marginal plates, *m*. These plates are formed at the extreme end of the ambulacral rafters, between the adoral rim of the lateral extensions of the terminal plates and the interbrachial region of the body. They follow the same law in sequence of formation as the adambulacral, but do not have the protection of the terminals in their early condition.

The first marginals to form appear in a stage between one with a single median dorsal and one with two median dorsals (Pl. IV. figs. 1, 2). It is a curved plate, extending on the actinal side to the interbrachial region and on the abactinal to the vicinity of the first median dorsal, *d*. On its dorsal region it bears a single spine (Pl. IV. fig. 2).

The first pair of marginals is firmly jammed in between the lateral extensions of the terminals and the interradial portion of the circumoral plates, and by its subsequent growth helps to push out the terminals in

the increase in length of the arms. A second pair of marginals is not formed until after the second pair of interambulacrals has appeared.

The forming marginals bridge the intervals between adjacent interambulacrals. They are larger than the interambulacrals, but not so massive, and form curved plates making the curve in the margin of the arms. Their number is not so constant as compared with that of the ambulacrals as with the adambulacrals, and in this respect even in very young stages they recall the marginal plates of the adult starfish.

Oral Ambulacral Plates. — The plates, or calcareous framework which surrounds the mouth of Asterias, date back to very early stages in the growth of the starfish (Pl. I. fig. 3). Rudiments of these structures appear while yet the starfish has a disk-like form, and before the complete absorption of the arms of the brachiolaria.

In the earliest condition in which these plates were seen there were but eleven other plates in the starfish body, and these were all found on the abactinal surface. These eleven plates are, of course, the single dorsocentral, the five terminals, and the five genitals.

The oral ambulacral plates appear on each side of the primitive extensions from the right water vessel, *rw*, which later form the five radial water-vascular tubes of the arms. They appear in pairs and are ten in number, a pair to each pair of legs.

In their earliest stages they are spiculate and elongated, their length running parallel with the walls of the water tube (Pl. I. fig. 3). This fact is an important one, for it recalls the condition which we have in the ossicles, or ambulacral plates, of Amphiura. I shall speak of this condition later. The elongated rods or spicules have later (Pl. II. fig. 1) small lateral branches, and a beginning of a network is to be seen. The two members of the pair never grow together laterally in the position that they are at first placed.

The condition of the water tube, when the first pairs of circumoral rods form, is briefly as follows. The tube has not joined about the mouth, as the brachiolaria is not yet fully absorbed. The five median water-vascular tubes, *rw*, are simple protuberances, without lateral appendages. The pre-divided water system is asymmetrically placed as regards the disk of the future starfish, and the five extensions do not project beyond the stomach of the brachiolaria. In the next form in which the circumoral calcareous rods appear, we find that the brachiolaria has been wholly absorbed, and the starfish has assumed a stellate form, brought about by an enlargement and growth of the terminals (Pl. II. fig. 2). While the oral plates were placed with their

lengths parallel with the median water tube, they are now at right angles to its course. The median tube has not yet extended to the extremity of the edge of the terminal, but has formed two and three pairs of lateral branches, — the first formation of the legs of the starfish. The ten oral ambulacral plates or rods, *am*, form a pentagonal network, not yet united, but already in the approximate position which it occupies in the adult (Pl. II. fig. 3).

The plates are crescentic, with convexity pointing outward, perforated, closely approximating near the middle line of the radius, and more distantly separated in the interbrachial regions of the starfish. As far as their general appearance is concerned, they resemble incipient ambulacral plates of later stages of Asterias, as in former conditions they resembled those of Amphiura.

In an older condition (Pl. II. fig. 3) of the oral ambulacral plates, the interbrachial ends grow together, and at the same time become very much more thickened in the interbrachial region. The ten oral ambulacral plates, *am*, now form a pentagonal ring about the mouth opening. In this stage the rudiments of two pairs of ambulacral rafters, am^1, have likewise appeared.

The outlines of the single member of the oral ambulacral ring of plates at present are as follows. Each oral ambulacral plate has the form of an elongated bar, enlarged at either end. The length of the bar is at right angles to the line of the radius of the arm. On the aboral side it is deeply concave, while on the adoral it is straight, slightly curved. The radial extremity is bifid, divided into an upper and lower branch (Pl. III. fig. 1). The interradial extremity is enlarged into a massive thickening, forming a club-shaped body whose aboral broad end abuts the lateral wall of the terminal. The mass of the thickened part of the oral interbrachial plate is on its actinal side, while on the abactinal side it is concave, in which concavity fits a heart-shaped plate, *ib*, later described as the odontophore. This thickening in the interbrachial region of the oral ambulacrals corresponds with the interambulacrals, and these plates represent interambulacrals of the oral ambulacral plates, although they do not seem to be formed as separate calcifications. In early conditions no spines are found on the oral plates or bars. No spines were ever detected in the ambulacral region of these bars, although in older conditions of that part of the oral plates which lies in the interradii spines were found, as in the other interambulacrals.

The subsequent growth of the interbrachial ends of the oral ambulacrals is as follows. They grow at the expense of the ambulacral orals,

forming elongated bodies whose greatest length lies in the direction of the interradius, or parallel to it. As their size increases, four spines form on each of these plates, two on the aboral and two on the adoral ends The existence of these spines would indicate that they are consolidated interambulacrals, and that interambulacrals as well as ambulacrals enter into the formation of the oral ring of calcareous bars.

*First Interbrachial.** — In very early conditions in the growth of the oral ring of bars, before the increase in size of the interambulacral ends of the circumorals, and before spines appear, there form in the interbrachial radii certain round or heart-shaped plates, which are thought to be the first sign of the odontophore.

These plates, *ib.* lie on the abactinal side of the adambulacral circumorals, in a space between them and the genitals, and on the adoral side of the circumorals. Their first form is round, or heart-shaped. As the growth goes on they are pushed more to the aboral region of the interradius, but never extend beyond the cover of the interambulacral ends of the circumorals, by which, in the increased compactness in growth of the calcareous network, they are almost wholly concealed when the starfish is seen from the actinal side.† This is the first time that the odontophore has been described in starfishes as young as Plate II. fig. 4. From their position of formation they seem to be homologous with interbrachials, which will be subsequently described.

The Ambulacral Rafters. ‡ — Under the name of ambulacral rafters all actinal plates of the rays, with the exception of the circumorals and the adambulacrals, will be included. The following plates are present when the first pair of ambulacrals begins to form: dorsocentral, *dc*, five genitals, $g^1 - g^5$, five terminals, $t^1 - t^5$, and ten circumoral ambulacrals, *am.* In addition to these the interambulacral circumoral and the odontophore, *ib*, are formed before the second pair of ambulacrals, *am.* The first of the median dorsal row of plates, *d*, appear just after the second pair of ambulacrals. The marginals, interambulacrals, and second median dorsal appear after the third pair of ambulacrals.

* The name odontophore, with which this is homologous, as pointed out by Ludwig, is illy suited for the first interbrachial plates on the actinal hemisome. The true name of these plates can hardly be known until there is some uniformity of opinion as to their homologies. The term interbrachial does not commit us to the theory that they are homologous with orals or with unpaired marginals.

† In certain deep water Asterids, according to Sladen, a part at least of the odontophore is visible on the actinal surface of the adult. In very young specimens of Asterias the same thing is true. The feature in the deep-water starfishes would seem to be embryonic.

‡ The plates referred to are commonly called ambulacrals.

The ambulacrals follow the law of formation of the other arm-plates, with the exception of the terminals. The first ambulacral to form is nearest the circumoral, and new plates are added aborally to the first formed. The new ambulacrals are protected by the cap-shaped terminals. The ambulacrals originate as elongated rods, with axes at right angles to the line of the radius. The two members of a pair do not necessarily arise simultaneously. The position of origin is nearer the centre of the arm, or nearer its median line than the periphery.

In the earliest condition in which the ambulacrals were seen, they had the form of small calcareous nodules, one on each side of the median line of the arm (Pl. II. fig. 3). In older stages these nodules elongate into bars, growing from the middle line towards the side of the arm on its actinal region (Pl. II. fig. 4). By an increase in the length of the ambulacral bars, they bridge the interval between the middle line of the arm and the lateral extensions of the terminals, although they never join the last mentioned structures (Pl. III. figs. 1, 2).

Each ambulacral bar has the following form. Near the middle line it is enlarged, while on the aboral and adoral borders it is concave, in order to leave an interval or space for the passage of the legs to the ampullæ.

As the growth of the arm of the starfish goes on, and new pairs of ambulacrals are formed, the terminals are pushed out more and more from the disk. At the same time the ends of the ambulacrals approach one another on the median actinal line of the arm, and ultimately become articulated together. Before, however, they join, they bifurcate on the median line, and form an upper and a lower spur, as in the circumoral calcareous ring. As in early stages of the starfish, there are only two rows of feet, one on each side of the median line ; the rows of openings for the passage of the feet are also in two lines. It is only in young starfishes of considerable size that we find four rows of openings between the ambulacral rafters. In all the specimens figured there are but two rows of feet.

The young stages of Asterias studied by me were never found to have spines on the ambulacrals, and neither in the oldest nor in the youngest was there any median row of plates or spines of an embryonic nature on the actinal side of the arm.

Second Interbrachial. — When the growing starfish, in which the arms have pushed themselves out to a considerable size, is looked at from the actinal side, there will be seen in the interradii, in the space left between the marginals and the abaxial end of the interbrachial ex-

tremities of the oral ambulacrals, a single interbrachial resembling the first (odontophore), but abaxial to it (Pl. V. fig. 8, ib^2). This is called the second interbrachial, ib^2. Other interbrachials outside (abaxially to) this were found; but in the genus Asterias the number and development of these interbrachials is not as great as in some other genera. The first of these interbrachials, "odontophore," might be regarded as homologous with the orals of the Amphiura. The homology of the others in Ophiurans is not clear to me. They are of course represented in other starfishes, where they are sometimes very greatly developed, imparting a characteristic form to the body, filling in the whole interbrachial region.

The remaining interbrachials may be numbered among early plates to form in the young starfish. They are, however, the last plates to form of all those which we have mentioned in our account of the early or primary plates of the body.

When the starfish of a stage like that shown in Plate V. fig. 7 is seen from the actinal region, an irregular triangular interval is seen in the interradius just outside the two interambulacral circumoral plates, *amd*. This interval is bounded by the adambulacral circumoral, *amd*, the first interambulacrals, ad^1, one on each side, and the laterals, also one on each side. In the centre of this space, on a line opposite the middle of the interambulacrals, the first interradial or interbrachial takes its rise. As the starfish matures, other interbrachials also form outside, aborally from that which has already appeared.

Connectives. — Under this name are included certain plates of the body and disk of the starfish, which bridge the intervals between the others, but which have a secondary place as compared with primary plates. There are connectives on the abactinal region of the arms, and others on the disk, but in either case they do not differ greatly from each other. In the connectives we have a multiplicity of calcareous plates, imparting a compactness to the abactinal hemisome. Their form, size, and number are variable, and their morphological importance of a subordinate character.

Spines. — The study of the primary spines of the young Echinoderm is one which in most accounts of the development is not given very great prominence, yet these bodies are in many genera among the first calcifications to appear, antedating in formation many plates which play a most important part in the determination of the external form of the animal. When the first spines appear in the starfish, there are only eleven plates present, five terminals, five genitals, and a dorsocentral.

The dorsocentral is hardly larger than a small calcareous nodule, and the genitals and terminals are but simple branched spicules. Not a single plate of the actinal region of the body has yet appeared. It will be seen that plates which have been regarded of importance in a discussion of the affinities of the starfish with other Echinoderms are not even present as a simple rudiment, when spines which few have yet considered of any great importance morphologically have begun to form, and are well developed in many cases. Are we justified in thus neglecting the spines, or have they no morphological meaning outside of a simple classificatory interest? The discussion of the meaning of the large size of the first-formed spines will be taken up later. It is necessary now for us to consider the size, arrangement, and distribution of these structures, their embryonic form, and their general mode of growth.

The spines originate as trifid spicules, and in their early stages are not to be distinguished from calcareous plates. The earliest spines (Pl. I. fig. 3, *sp*) to appear are those at the outer rim of the terminals of the young starfish, peripherally to these plates. They are at first ten in number, or two to each terminal, and by the time the notches which indicate the interbrachial regions of the future starfish are incised, the number of immature primary spines has increased to nine. Later, when the number of ambulacral rafters has grown to six (three pairs), there are six very prominent spines on the outer border of the terminals. According to A. Agassiz, these spines are more or less fan-shaped, and recall those of certain Echinoids. The dorsocentral, for a long time after its first appearance, bears a single long and prominent spine. This calcification is jointed to the centre of the dorsocentral on the aboral side, and later other primary spines are added to the dorsocentral. The genitals (basals) have at first three long, slender spines, which originate while yet the starfish is borne by the brachiolaria. The spines of the medial dorsal plates of the arms are prominent and single at first, each situated in the middle of the plate upon which it is carried. The lateral or marginal plates, *m*, of the arms bear long, stout, single spines. Each interambulacral plate, *ad*, has at first a single spine. No spines were ever observed in the ambulacrals, but the extremities of the oral ambulacrals in the interbrachii bear four spines, two of which lie on the edge adjacent the mouth. The so-called odontophores * were

* From the position which they early occupy, it is not to be wondered at that spines are not developed on the first interbrachials or the odontophores. They are covered on the actinal side by the interbrachial ends of the oral ambulacrals, so that spines could not be formed.

not observed to carry spines, and the interbrachials, in their younger stages at least, are destitute of these structures.

With the advancing growth of the starfish, the number of spines on the primary plates increases, and new spines are formed on new plates as they appear. The later formed spines, however, never have that prominence so marked in the younger and primary plates, but appear more compact, and more like the spines of the adult Asterias.

Pedicellariæ. — The pedicellariæ, *pd*, were first observed on the terminal plates in a stage of the starfish in which there were four median dorsals (Pl. IV. fig. 3). They were then confined to that plate, being absent on all others. In an older starfish, or one with seven median dorsals (Pl. IV. fig. 4), they were likewise found in clusters on the second marginal plates, m^2, and one or two were likewise seen on the plates, m^3, between the second marginals and the terminals. Although in both these stages large spines exist on the median dorsals, *d*, there are no pedicellariæ as yet formed upon or near them. Like the spines, the calcifications of the pedicellariæ are at first wholly separate from the plates from which they rise. Unlike the spines, however, their calcification is from the first double, or split longitudinally into two separate parts.

Stone Canal. — The calcifications in the wall of the madreporic canal were observed in a larval stage before the external modifications of the plate through which it opens were evident or had appeared. It consists of a delicate tubular network of calcifications, formed by a lacework of calcareous spicules, which appear to arise from many centres of formation. They appear to form in the wall of the tube itself. I am unaware that any one has described the stone canal in a young starfish in which there were but seven median dorsal plates, yet it is well marked at that age.

4. Comparison with other Asteroidea.

It is here intended to consider certain relations between the plates of Asterias and the observations and comparisons which have been made by others on the plates of young starfishes. The study of the calcareous formations of the adult and their history from the time when they first appear has engaged the attention of several naturalists, and many different conclusions have been arrived at in this study. With these recorded observations and interpretations I have been able to compare my own on Asterias, and their concordance has strengthened my belief

in them. In one or two instances, however, there are differences, either of observation or of interpretation. It will perhaps be profitable, before we can discuss the relationship of Asterias with Ophiurans, that these differences and concordances among Asteroidea be considered. The subject deals with calcareous plates only.

The most important observations of the way in which the plates of Asteroids develop are those of Krohn, Thomson, A. Agassiz on Asteracanthion, Ludwig on Asterina, and Lovén on *Asterias glacialis*. The way in which the plates of Asterina develop is as well known as that of any other Asteroid, if not better. As this development of Asterina pertains to a starfish without a nomadic brachiolaria, and as Asterias has an indirect development with nomadic brachiolaria, it is interesting to compare the formation of the plates in the two types, and to note the differences which occur. Whatever the character of the metamorphosis of a starfish may be, — whether it has a nomadic brachiolaria, as Asterias, or carries the young in brood-sacs, as in Pteraster, — it would appear that the sequence of the growth of calcareous plates is little affected by it. How much the abbreviation in early development affects the sequence in the growth of plates is yet to be proved, and a complete series of the young Asterias to compare with Asterina may give us valuable information on this point. The figures of Asterina by Ludwig, and those of Asterias by Agassiz, Krohn, Thomson,* and Lovén,† in a way supplement each other, yet much still remains to be done on late stages of both genera.‡

For a comparison of the way in which the plates of the abactinal hemisome of the body of Asterias develop with those of other Asteroids, I have little to add to what is known as far as the dorsocentral is concerned. The various authors who have written on this subject do not emphasize the fact that it is formed after the terminals and genitals, or

* Krohn and Thomson figure and describe isolated stages of growth. Agassiz considers the whole subject of the development.

† Lovén figures only later stages with stellate form.

‡ It would appear from the relative time and sequence of the appearance of plates in related genera of Ophiurans being very different, that it is not safe to rely upon a similarity in time when calcifications appear in the comparisons of homologous plates. Other naturalists have already commented on this fact. A diversity in the time of the appearance of homologous plates in related species seems to me paralleled in the fact that in two Asterids once thought to be generically the same, and even now, if their adult features alone are examined, regarded as generically identical, one, *A. tenera*, has no nomadic brachiolaria, and the other, *A. berylinus*, has such an elaborate metamorphosis with this stage.

that it antedates all the plates of the actinal hemisome. Agassiz supposed it to be formed after the other ten abactinal plates, and Ludwig * does not say that it is or is not formed at that time.

The time of formation and mode of growth of the terminals, at the tips of the arms, seems to be the same as already described by A. Agassiz and Ludwig. Agassiz found them to form before the genitals, which is true also in my larvæ. I cannot verify the statement that the terminals ever fuse with each other, as described by Agassiz. The arrangement of spines on the terminals differs somewhat from those of Asterina.

According to Ludwig (p. 50, *op. cit.*) one of the interradials (genitals) precedes in time of formation and size the other genitals and the terminals. This is the genital which later forms or fuses with the madreporic plate. This predominance of the genital contiguous to the madreporic opening was not noticed in Asterias, although the relative distance and general situation of this plate as compared with the madreporic opening are about the same as Ludwig describes for Asterina.

My observations on the growth of the plates of the abactinal region of the arms resemble those recorded by A. Agassiz, Lovén, Ludwig, and Viguier. The calcifications of the body in the abactinal hemisome also resemble, with some exceptions, those already described. According to the first author (p. 37), in an early condition after the eleven abactinal plates were formed "the whole of the abactinal surface has become coated with a very fine granular deposit of limestone." This formation was not seen in the specimens of Asterias which were studied.

The observations on the mode of formation of the oral ambulacrals

* His youngest stages show eleven plates, and in the text he speaks of them as if the "Centrale," dorsocentral, was synchronous in formation. (See Entwicklungsgeschichte der *Asterina gibbosa*, Forbes, Zeit. f. Wiss. Zool., Vol. XXXVII.)

The homology of the calcifications of the pluteus of Ophiurans and Echinoids with calcifications in the stem of the Crinoids would seem far-fetched. The spines of the pluteus are secondary developed structures, and it is believed by some that they have no phylogenetic significance. The fact that they are wanting in the brachiolaria of Asterias would look that way, but in Amphiura they are represented *before* the larva leaves the mother. It is possible in this instance to believe either that Amphiura is descended from a genus which had a pluteus with spines, and in its abbreviated metamorphosis the rudiment of the spines only remains, or that the plutean spines show relations with other groups outside the Ophiurans. The latter conclusion does not appear absurd, and it may be possible later to show that there is an homology between the stem of a Crinoid and the plutean spines of an Ophiothrix.

resemble those of Ludwig on Asterina,* and Lovén's figures of *A. glacialis*,† but differ somewhat from Agassiz's. A. Krohn ‡ was one of the first correctly to figure the situation and early form of the oral ambulacrals of the starfish in young stages in its growth. His figure of the ten first formed oral ambulacral plates in the starfish found in Bipennaria correspond closely with those of Asterias which I have represented. He also figures the spines of the terminals, but does not represent the terminals as they exist in Asterias.

Sir Wyville Thomson's figure and description§ of the early forms of the ambulacral rafters of *Asteracanthion violaceus* closely resembles what I have seen in Asterias. His figure of the oral ambulacrals and the ambulacral rafters corresponds with mine. There is not as close a likeness in the plates of the abactinal side which he has figured and my own. The first dorsal seems more prominent in one than in the other. Both of his figures, represented from the actinal and abactinal hemisomes, are regarded as important contributions to our knowledge of the early form of the calcareous plates of Asteroids.

Metschnikoff‖ has published very instructive figures of the young and stellate forms of a starfish. In Plate XI. fig. 8, he represents the earliest form of the ambulacral orals about as they appear in Asterias. They have here the form of simple calcareous spicules. The spines of the terminals in this stage are also well shown. Another figure of a young starfish by the same author (Pl. XII. fig. 1, A) represents five terminals, an inner row of six genitals, and a dorsocentral. The mad-

* It may be borne in mind that the mouth of Asterias is "ambulacral," i. e. formed for the most part of modified ambulacrals, while Asterina is classified as "adambulacral," — mouth formed of both ambulacral and adambulacral. It is consequently necessary that the young stages of Asterina have adambulacral calcifications distinct from ambulacral in the formation of oral plates. It would seem from Ludwig's figure (fig. 98) and his lettering as if it was formed in this way. In Asterias, however, similar plates are formed from the interradial ends of the ambulacrals, and not as separate calcifications. If I am right in my observations, it would seem that Asterias has an ambulacral mouth from the early stages of growth.

† Études sur les Echinoidées. K. Svensk. Vetensk. Akad. Handl., Stockholm, Vol. XI. Pt. II.

‡ Krohn, August. Ueber die Entwickelung der Seesterne und Holothurien. Arch. f. Anat. Physiol. u. Wiss. Med., 1853.

§ Thomson, C. Wyville. On the Embryology of *Asteracanthion violaceus*, Quart. Jour. Mic. Sci., I., 1861.

‖ Metschnikoff, E. Studien über die Entwickelung der Echinodermen und Nemertinen. Mém. Acad. Imper. Sci. St. Pétersbourg, Vol. XIV. No. 8.

reporite is represented in the same ring as the terminals, and in position is a separate plate from the genitals. The genital which occurs in the same interradius is double.

If this condition or arrangement is found on more extended observations to be the exact relation, it may lead to much light on the whole question of starfish morphology; for if the madreporite is not a genital, but a distinct plate, the fact adds strength to the belief that the oral of Amphiura is the homologue of the odontophore, while the basal of Amphiura is the homologue of the genital of Asterias. It may render it necessary for us to regard the madreporite in starfishes as ordinarily described as a consolidation of genital and madreporite, which would somewhat affect accepted homologies. The separate calcification of the stone canal, and the eccentric position of the madreporic opening as compared with the genital, point to to a compound character of the madreporite.

A. Agassiz's account of the way in which the ambulacral and interambulacral plates of the arms of starfishes are formed, differs from what I find in Asterias. He says (pp. 91, 92), "In the case of the young starfish, the radial plates of the abactinal system which form the dorsal part of the arms gradually extend towards the edge of, and down on to the actinal side, enclosing the water system little by little, and finally, as has been described, covering the ambulacral tube, leaving only openings for the passage of the tentacles. . . . In the starfishes, the actinal plates formed by the bridges separating successive pairs of tentacles become resorbed along the central line, the edges forming inwardly by spurs the true ambulacral plates, and the plates which little by little develop so as to form the edge of the arms are likewise formed from the plates originally a part of the abactinal system. Those which are on the outside of the tentacles become the interambulacral plates, but differ in no way from the plates forming the sides of the arms." *

If I rightly understand his account, there is considerable difference between the way in which ambulacral and interambulacral plates form in the starfish which I studied, and those which he describes. The

* It is hard to reconcile this view of the way these plates (ambulacral) form with the figures of them by Krohn and Thomson. Agassiz's figures (Pl. VI. fig. 12, Pl. VII. fig. 1, Embryology of the Starfish) of the plates of the actinal side of the arm differ from those of Krohn of a starfish from Bipennaria, and of Thomson of *A. violaceus*. They also differ from mine. The separate ambulacral rafters and oral ambulacrals are not represented, but the actinal calcareous plates are represented as joined together.

main difference is, that in the Asterias which I studied the plates on the actinal side of the arm originate on that side, and there is no growth downward from the abactinal surface enclosing the water system. The ambulacral rafters and interambulacrals originate as separate calcifications on the actinal side of the arms, while no absorption of plates previously formed was observed.

There is a close similarity in the early formation of the actinal plates in Asterias and of those of Asterina, followed by Ludwig, and my interpretation of some of the plates of the mouth is in most cases the same as his.

Ludwig says (p. 49, *op. cit.*) that he is the first to make known the primary position of the ambulacrals.* The difference in the early form of the first and second pairs of ambulacrals, or those which form the oral ring, is not especially considered by him, and his account does not extend to the growth of the ambulacrals formed subsequently to the oral or first pair.

It was not possible for me to observe any relationship in the time when the members of the five pairs of ambulacrals form, or their sequence, as he has done in Asterina, although I have repeatedly found young starfishes in which one pair of ambulacrals (oral) smaller than the remaining, or in which one or more members of the five sets were missing.

The five pairs of plates which Ludwig (*op. cit.*) letters JA in his account of Asterina are called by him interambulacrals. By this term it is understood that he means what are here called marginals. In the development of these plates Asterias closely resembles Asterina.

Adoral to these plates lie five other plates, a single plate in each interradius. These are the first interbrachials, and are regarded as the odontophores of authors. They are called the heart-shaped plates from the shape which they have in the young Asterias. In Asterias the interbrachial ends of the oral ambulacrals arch over the heart-shaped bodies before the "lateral plates" are developed.†

* Ludwig was the first to show how the ambulacrals originate in Asterina. The form and early condition of the oral ambulacrals of an Asterias-like starfish with a brachiolaria was given by Krohn in 1853. Thomson (*op. cit.*) in 1861 figures correctly the first form of the ambulacrals in *A. violaceus*. It would therefore seem that in genera besides Asterina the subject had already attracted observers.

† Ludwig was at first of the opinion that these odontophore plates are "Intermediäre Skelettplatte," which I interpret to be the same as "orals"; he later sup-

The position of the newly formed interambulacrals as regards the terminal is similar in Asterina and Asterias.* In Asterina, from Ludwig's diagram, I should judge that these plates arise near the outer ends of each pair of ambulacral rafters, so that a line through them would pass through the length of the rafter. In Asterias, however, the interambulacrals arise in the interval *between* the outer ends of the early formed ambulacral rafters.

Plates homologous to the under basals of Crinoids are recognized by Sladen † in several species and genera of Asteroids, including *Asterias rubens* and *A. glacialis*. I have been struck in the examination of figures of deep-sea starfishes to see how close, in some instances, the likeness between the test of certain of them and that of the young Asterias is. The young and adult of Zoroaster seem closely to resemble certain young stages of Asterias. Sladen comments on the "unmistakable crinoidal facies" which the young Zoroaster has, and regards a young stage of this Asterid as highly suggestive of the Ophiuroid genus Ophiopyrgus. Whether the resemblance between the young Asterias and the young Zoroaster can also be interpreted as a crinoidal facies, I leave to those more familiar with the Crinoids to consider. The simple arrangement of plates in Zoroaster is an embryonic feature.

There is some danger in affixing to the plates of starfishes names of plates which are current among students of Crinoids. While it may be held to be proper to do so, if the Crinoids represent the ancestral condition of Echinoderms, it might lead to error if they are simply specialized or degenerate descendants of other and older groups.

posed them "Unpaare Interambulacralplatte." It is thought that he means by the latter the marginal plates.

* Fig. 97, Plate VII., of Ludwig's paper on Asterina would seem, from the position of the terminal as regards the feeler, F, to be a view from the abactinal side. Such a conclusion is likewise supported by the relative position of the plates, A^2, or second pair of ambulacral rafters. If, however, the view from which the figure is seen is from the abactinal side, it would seem as if other abactinal plates would be represented. If they were figures of Asterias of the same age, such plates certainly might be expected to be visible. Perhaps the term "bei tieferer Einstellung" explains the peculiar arrangement of plates and the loss of the abactinals. I am unable to understand the figure, since the view is said to be from a preparation (fig. 96) which is shown from the actinal side.

† On the Homologies of the Primary Larval Plates in the Test of Brachiate Echinoderms. Quart. Journ. Micros. Science, Vol. XXIV., new ser., 1884.

Judging from Sladen's figure of *Zoroaster fulgens* (fig. 16), it seems that what he calls the "underbasal" is also represented in the abactinal hemisome of a young Asterias.

It is a most important thing to know more of the early formed plates of the genera Caulaster, Perr.,* and Ilyaster, D. & K., in which we have appended to the middle of the abactinal zone a short peduncle. It would seem that this peduncle is comparable with the stem of a Crinoid. In a young Ctenodiscus a protuberance in the same place as the peduncle of Ilyaster has been noticed, but I have never seen it as long as figured in Ilyaster. As Ctenodiscus is a common starfish off the New England coast, it would present a most instructive genus for the study of the homology of the early formed plates of a starfish with an abactinal prominence.

If it should be shown that this appendage to the abactinal region of the genus Ilyaster is a remnant of the ancestral Crinoid stem, it might be supposed that the Asteroidea have descended from crinoid-like genera. It may likewise be true that the Crinoids are highly specialized and descended from certain starfishes or Ophiurans. In this case, perhaps, the arrangement of apical plates in the larval starfishes is the most primitive, and may determine the nomenclature of the Echinoids.

The pedicellariæ of Asterias are relatively somewhat larger in the young than in the adult. In their early condition they are short and stunted, clavate, with at least two centres of calcification, which later form the two jaws. Unlike the primary spines, the calcifications in each pedicellaria are not consolidated, but double from the very first. The theory that the pedicellariæ are homologous to spines, renders it necessary to compare calcifications which differ in shape from the very first, and also to compare a primarily single with a double calcification. Neither of these difficulties is necessarily fatal to the theory, nor does the mode of development of spines and pedicellariæ give wholly satisfactory proof of the theory.

The growth of the spines on the calcareous plates of Asterias resembles that of the same structures in Asterina, as described by Ludwig. In the case of the spines of the primary plates they arise as separate calcifications, and are not extensions from plates already existing.†

* Mémoire sur les Étoiles de Mer recueilles dans la Mer des Antilles et le Golfe du Mexique durant les Expeditions de Dragage faites sous la Direction de M. Alexandre Agassiz. Nouvelles Archives du Museum, 2 ser., Vol. VI.

† The "ambulacral spines" observed by A. Agassiz on the outer edge of the ambulacral plates were not observed in Asterias. Is it not possible that these spines belong to the "interambulacrals"?

The calcification of the stone canal is not treated by other naturalists who have studied the early form of these organs in younger stages of Asteroidea; so that it is not possible to compare my observation with others as far as this structure is concerned.

The growth of the calcifications of the pedicellariæ in Asterias is the same, or nearly the same, as has already been recorded by A. Agassiz. No histological studies were made of these organs, and my attention was not turned to their minute anatomy.

A. Agassiz found that the madreporic opening is placed on the "actinal side in the angle between two rays," * and that it is protected by a thick funnel-shaped projection. There seems to be a difference in the position of this opening in some of my larvæ from those which he studied, for in the younger larvæ of Asterias the madreporic opening does not lie on the actinal side of the larva, even in considerably advanced stages. The position of the madreporic opening is of course a most interesting thing in morphological studies of the young starfishes, and more observations as to its position are needed.

In the figure already referred to which Metschnikoff gives of the abactinal side of an unknown starfish, the madreporic body appears on the very margin of the disk of the starfish, and would seem intermediate in position between a madreporic body on the actinal and on the abactinal surface. In Ludwig's figure (fig. 94) of the young Asterina in which a stellate form has been taken on, the madreporite (P) is abactinal. In some of my older stages I was unable to discover the madreporic plate, but believe it in all cases abactinal.

5. Homology of the Plates of Asterias with those of Amphiura.

Of all the Ophiurans the growth of the plates is best known in a viviparous genus, *Amphiura squamata*, Sars. While it is desirable to know more of the sequence and method of formation of the plates in an Ophiuran which has a development through a pluteus, the genera which present this condition have as yet not been much studied as far as the growth of plates is concerned, and our knowledge of the Ophiuran plate development wholly relates to Amphiura.† In comparisons

* *Op. cit.*, p. 45.

† The author is not of the opinion that any very great exception to the law of the growth of new plates is brought about by what is called abbreviated development in Echinoderms. In essential points the growth of the calcareous plates in Asterias and Leptasterias, genera representing two types of development, is the

between stellate forms of the two groups, Ophiurans and Starfishes, I have chosen, therefore, Amphiura on the one side and Asterias on the other as representatives. It would seem as if it were necessary carefully to compare the stellate forms of Echinoderms before we can pass to others, when the external forms are so varied. It may seem as if the difficulties in a comparison of Ophiurids and Asterids would be small, but even here we find very great differences in opinion as to the homology of certain plates, and a variety of interpretations upon structures of primary origin. While it is not proposed in this paper to go beyond a comparison between stellate Echinoderms, it is believed that a more accurate conception of the relationship of plates is possible than that ordinarily accepted. There is range enough in the modification of plates in Ophiurans and Asteroids to call for the best possible statements of their relationship in the two groups.

The following theses may be stated in a tabular form, to indicate the line of discussion which is to follow. Plates of Asterias and corresponding plates of Amphiura are placed side by side.

Asterias.	*Amphiura.*
Dorsocentral.	Dorsocentral.
First dorsal ?	Radialia.
Genital.	Basal.
Oral ambulacrals.*	Spoon-shaped plates.
Interbrachial ends of oral ambulacrals.	Adambulacrals (1 and 2).

same. It is not intended to compare Asterias with any Ophiuran except Amphiura. The many problematical questions which have arisen in a comparison of Amphiura and Crinoids are also passed over in silence. My object in this paper is to see if it is possible to arrive at a better idea of the homologies of the stellate Echinoderms. A discussion of the homologies of the plates of either with those of Echinoids, Crinoids, or Holothurians is not proposed. Amphiura is chosen for a comparison, for the reason that the development of its plates is better known than those of other Ophiurans. From the statements of those who have written on the development of an Ophiuran from the pluteus, it would seem that there is some difference in the sequence of the plates in Ophiurans with and those without a pluteus, but the amount of difference is yet to be made out.

In this connection, it seems to me that published statements about Ophiophragmus by Mr. Nachtrieb have an interest. Nachtrieb (Studies, Johns Hopkins University, Vol. IV. No. 2) finds that Ophiophragmus has a "development without pluteus." He says he was able artificially to fertilize Ophiophragmus. This is the first time, I believe, that an Ophiuran without pluteus has been artificially fertilized; and, judging from the statements which he makes, the development of Ophiophragmus must be very peculiar.

* Under this designation I refer to the plates which resemble ambulacral rafters, surrounding the mouth.

(Odontophore) First Interbrachials.	Oral.
Other Interbrachials.	
Connectives.	Wanting on arms.
Terminals.	Terminals.
Dorsals.	Dorsals.
Dorsolateral.	Wanting.
Marginal.*	Wanting.
Ambulacrals.	Ambulacrals.
Interambulacrals.†	Laterals (Adambulacrals).
Under-basals ?	Under-basals.

The ventrals of Amphiura and the plates of the stone canal and pedicellariæ of Asterias are not common to the two genera.

Spines (embryonic) are present in the laterals (adambulacrals) of Amphiura. They are not found in the ambulacral rafters of Asterias.

It will be noticed in the above list, that two adambulacrals of Amphiura (1 and 2) are designated as the same as interbrachial ends of the oral ambulacrals of Asterias. In Asterias they resemble other ambulacrals, except that on their interradial ends they bear spines, while in Amphiura they more closely resemble adambulacrals, and so they were called by Ludwig. It will probably be said, that they are either ambulacral or interambulacral (adambulacral), and abler persons than myself may be able to show that the oral ambulacrals of Asterias are different from the oral adambulacrals of Amphiura. I confess, however, that I am unable to see that they may not be the same plates, now modified in one way, now in another. They are the most difficult plates to compare of any in Asterias and Amphiura. Without being able to make up my mind whether or not there are plates in the young starfish homologous with the torus and teeth of Amphiura, I think it not improbable that these structures may be homologous with the "Aristotle's Lantern" of urchins, but I am not willing yet to venture that statement. There are in certain genera of Asteroids, of course, teeth which may be compared with the teeth of the Amphiura; but whether they are homologous is doubtful.

P. Herbert Carpenter, in his paper on the growth of the calcareous plates of Amphiura, has pointed out differences in the time of appearance of the same plates in the American and European varieties of *A. squamata*. I regard this as a very fruitful field for morphological study. The recognition of a great difference in the time of the appearance of homologous plates among Echinoderms seems to me an important one. There is considerable variation in the time and sequence of

* Interambulacral of some authors. † Adambulacrals of recent authors.

appearance of homologous calcareous plates in genera closely allied to each other, which certainly looks as if the difference in the time of appearance of plates is no valid objection to a strict homology of those plates. How much a recognition of this principle may change or modify existing ideas of Echinoderm morphology, as far as the plates are concerned, remains to be seen. It is possible that some of the differences in the sequence of the plates of Asterias as compared with other genera of Asteroids may be explained in this way. If we recognize so much difference in the time of the appearance of homologous plates in genera closely related, does it not call for great caution in this particular in the comparison of genera of different groups? It does not seem too much to say, that an acceleration or retardation in the time of appearance of *primary* plates may have led to essential differences in the external forms of Echinoderms. On the other hand, it is very strange if geographical distribution has brought about such a great difference in the sequence of plates as that which Carpenter finds between the American and European forms of *A. squamata*. It seems as if there must be some mistake in the identification either of the European or American specimens. As far as external form goes, my Newport specimens closely resemble *A. squamata*, and specialists in the study of Ophiurans have so identified them for me. Shall we call the American and European representatives different species or different genera, or does *A. squamata* in Narragansett Bay depart so widely from the same in European waters as far as development goes?

Dorsocentral. — There seems to be a uniformity of belief that the middle plate of the abactinal region of the body is homologous in Asterias and Amphiura. The only essential point of difference is the presence of a large spine in the young Asterias and its absence in Amphiura. This, however, is not thought to be of importance enough to have any morphological meaning. The author has no doubt that the dorsocentral forms in the same relative position in both genera, as shown by the observations already recorded. Whatever objections, therefore, might be urged on the ground that the sequence * is different, are not regarded as fatal. The name dorsocentral is well chosen, but should not be confounded with the centrodorsal of Crinoids.

Genitals. — The author homologizes the first ring of five plates, which form in the interradii of both Asterias and Amphiura, with each other.

* The only plates of Asterias which can be homologized with the radialia of Amphiura develop in Asterias *after* the dorsocentral. This fact probably has no morphological meaning.

There would seem to be no expressed variety of opinion on this point among those who have written on the subject; the only important question which has been raised being whether the term "genital" be an appropriate one to designate them, and whether their fate is the same. It is important, however, for us to call attention to this fact in regard to the so-called genitals in the two genera. While they are both primary plates on interradii, the absence of primary radials in Asterias has brought them to occupy a different position as regards the first formed plates in Asterias and Amphiura. For illustration, in Asterias they form an inside ring in comparison with the primary plates (terminals); in Amphiura they form an outside ring compared with primary plates (radials); they form an inside ring as compared with terminals in both. The relationship of one of the genitals to the madreporic opening would seem to show that the ring of plates of which this is a member is the same in both cases. Ludwig regards the first plate in the dorsal hemisome in the interradius of Amphiura as a madreporite. If he is right, there is no doubt that the first ring of plates in the interradii in Amphiura and in Asterias are the same.

In considering these plates as genitals, too much importance cannot be attached to the fact that no one has yet satisfactorily traced them to plates with the genital openings in starfishes. It is certainly a form of *a priori* reasoning to characterize them as genitals from the fact that they are the first interradials and occupy a similar position to the genitals of Echinoids. The one thing which we really know is that in Asterias one of these first interradial plates bears a definite connection with the madreporic body, and that it later occupies a similar position in one of the interradii that the genitals do in the other. Is it not a jump at a conclusion to suppose from this that they are necessarily genitals? If one should say that other interradials form the genitals, there are no observations to show the error. That the first (orals) plates of the interradii in Amphiura are genitals, we have even less to support our assumption than in Asterias. One of these plates, according to Ludwig, is perforated by the madreporic opening, and it is therefore supposed to be a madreporite. All five are later consolidated in the system of plates about the mouth, and bear no relationship to the genital openings. Obviously these cannot be the same as the genitals of Asterias, if genitals are homologous in Asterias and Amphiura. We are consequently driven to this position: the first formed interradial plates on the abactinal hemisome of Asterias do not enter into the formation of the mouth; they occupy a position which would indicate that they are genitals, and

one of them is early brought into connection with the madreporic opening. The plates of Amphiura which are in an homologous position appear not to have any relation to the genitals of the adult. One of them is a madreporite. The ultimate fate of both in Asterias and Amphiura is conjectural, but probably different.

In other words, while the genital of a starfish may be brought by its growth into intimate union with the end of the stone canal or with the opening of the madreporic tube, it may readily be seen that in Amphiura the oral, a plate of totally different homology, might have the same relation without the same homology. It would not make these plates homologous, i. e. genital and oral. Even if in Brisinga, with its ophiuran and starfish affinities, the madreporic opening is found on the odontophore, it is not necessary to regard the odontophore as a genital. The whole thing of course hinges on the acceptance or denial of the dictum that the presence of the madreporic orifice means homology of the plate through which it opens. While many naturalists in whose opinion we have the most confidence hold that it does, that the existence of the madreporic opening in a plate settles its homology once for all, to me it leads in some cases to insurmountable difficulties. It seems to me that the objection to the homology of the genitals of Asterids with the orals of Amphiura is well taken, if its defenders adopt the theory that the odontophore is an oral; for the genitals of starfishes are certainly not odontophores, even if in Brisinga one of the odontophores bears the madreporic body, or is a madreporite. The mistake seems to me just here: the madreporite may not be one of the genitals, or homologous with them, even in Echinoids, but is rather to be considered a separate plate, which may have connection with one of the heart-shaped bodies which form the odontophore. Ludwig was, I think, right in a comparison of the odontophores of Asterids with the orals of the Ophiurids. A. Agassiz has expressed the thought that the oral, or the plate we now call the odontophore, is an interbrachial, an homology which is sound, in the light of the development. The fact that in its early formation that genital plate which is nearest the madreporic opening forms wholly independently of the structure in question, has a meaning. In its early condition this plate is not penetrated by the tube in Asterias; but it is only later, after the brachiolarian notch has been considerably reduced in size, that the spicules begin to grow around the opening to enclose it. It is not until the stellate form has been assumed, and the arms have reached a considerable development, that the madreporic plate appears. It may be said that all the primary plates of the body

— viz. terminals, dorsocentral, genitals, spines, and even ten of the oral ambulacrals — have appeared before there is any calcification about the terminal opening of the madreporic tube. Does not this fact call for extreme caution in regard to statements that would lead us to homologize the madreporic plate with a genital rather than any other Asterid plate? Another thing, the outer edge of the genital grows around the end of the madreporic body to enclose it, and the stone canal forms before there is any cribriform plate over the opening. There is yet one fact which ought to be taken into consideration with those mentioned; viz. four interbrachials (odontophores) form at first, and the lower end of the madreporic canal occupies the homologous position of the fifth. While this fact does not demonstrate the homology of the madreporite, it is thought to have a bearing on the subject. The madreporite is not in intimate union with the odontophore after the odontophore forms, but it lies in the same interradius.* I venture to say that, if it is not in some kind of connection with the odontophore in Asterias, as Perrier says it is in Brisinga, it certainly is very close to it.

Sladen (*op. cit.*) finds no morphological relation between the odontophore and madreporite in Brisinga. While we may or may not subscribe to Sladen's criticisms of Perrier, he does not in either case seem to me to prove that there is "no morphological relation" between madreporite and odontophore, for when we go to very young stages in the growth of Asterias, we find a very intimate connection between the madreporite and odontophore.

As all the other odontophores of Asterias form on the actinal hemisome, and the plate which occupies a similar position in the interradius has a like position of origin, it would seem that Brisinga differs very considerably from Asterias, as far as the formation of the madreporite is concerned. In my specimens I certainly detected the odontophore of the interradial in which the madreporic body is found on the actinal hemisome, in the same relative position as the other odontophores. At the same time the genital (g^1) had not grown around the opening of the madreporic tube. Here, then, were two separate plates on opposite ends of an axis of the body. One could not be the other morphologi-

* Obviously, from the fact that one of the genitals grows around the madreporic opening, we are not obliged to regard this genital itself as homologous with a madreporite. We might easily suppose the primary separation of the madreporic opening and this genital much greater, and the stone canal so reduced that the madreporic body occupies a position which it is said to have in Brisinga.

cally. If the former is a madreporite, the latter is not; if the latter is a madreporite, the former cannot be. What additions now take place? (1) The genital grows around the opening of the madreporic tube. (2) The calcifications of the stone canal form. Neither of these events makes (g^1) the first genital a homologue of the odontophore, the homology of which preserves its distinctness whatever occurs.

In the case of the orals of Amphiura, it is found that one of them grows around the madreporic opening in the same way that one of the genitals grows in Asterias. It seems to me that this fact alone does not make genitals and orals homologous, and does not prevent the homology of orals of Amphiura and odontophores of Asterias.*

A comparison of the odontophore with the oral of Amphiura was made by Ludwig. According to Carpenter, he no longer holds that view, although Carpenter does not say what plate in Ophiurans Ludwig now regards as the homologue of the odontophore. As "interambulacrals (marginals)" are wanting in Ophiurans (Amphiura), it is difficult to interpret what plates here correspond with the unpaired marginals of the starfish. Perhaps Ludwig might still consistently hold that while the odontophore is an "Unpaare Interambulacralplatte," it is still a homologue of the orals of Amphiura where no marginals like those of the starfish are found. I believe that the first interbrachial (odontophore) is homologous to the oral, but do not say that Ludwig now holds such a view.

Sladen holds that the presence of the madreporite in a plate does not mean homology of that plate among Echinoderms.† It does not lie in the genital in certain starfishes, and it is disconnected with the orals in

* Waiving the difference of opinion of Sladen and Perrier (Compt. Rend., Vol. XCV., July 10, 1882), — the latter of whom holds that the madreporiform body in Brisinga is always formed on one of the odontophores, and the former, that no connection whatever exists between these two bodies, — is it not possible to conclude that we may have, in this ophiurid-like starfish, a genus in which the odontophore, like the oral of an Ophiuran, has been modified by its proximity to the madreporic opening, even if no connection has resulted?

† In this connection it may be well to call attention to the migration of the madreporic opening in Echinarachnius along an interradius from the edge of the disk towards the centre, as shown in my paper on the development of this Clypeastroid (Bull. Mus. Comp. Zoöl., Vol. XII. No. 4). A. Agassiz had already shown the migration of the periproct in the same genus (Bull. Mus. Comp. Zoöl., Vol. III. No. 9, p. 295). The madreporite moves from the margin of the disk to the centre; the periproct of Echinarachnius moves from the centre to the margin. It might better be said in regard to the madreporite, that by the growth of plates about it the madreporic body is pressed to the centre from the margin.

Astrophytidæ. His reasoning seems to me conclusive, and I do not regard the madreporite as a fixed point of reference in Echinoderm morphology.

Terminals. — The terminals in Amphiura and Asterias have so many points in common that I do not hesitate to regard them as morphologically identical. That they do not appear at the same time as compared with the other primary plates does not appear of importance enough to destroy the argument for their identity built upon their many resemblances of mode of growth, position, and relation to the median water tube of the ray.

Sladen considers that the occurrence of plates which he calls "under-basals" in the Asterid nullifies Studer's argument that the arrangement of primitive plates in Asterids corresponds with the monocyclic Crinoids. I do not subscribe to Studer's idea, but on the other hand I cannot but ask if Sladen has not overestimated the morphological value of his supposed discovery of the "under-basals" of Asterids in this connection. It may be well to remember that in Asterias the plates which Sladen likens to the Crinoid "under-basals" do not appear until after at least the Asterias may have had a monocyclic stage. At the time the "under-basals form," we might suppose that the starfish had passed out of, or become more developed than, the "monocyclic stage."

From their place of origin and their subsequent growth the terminals of Asterias and Amphiura are probably homologous. Moreover, it is probable that these plates are not to be compared with the other plates of the arm, which originate between them and the axis of the body. It had seemed to me possible to find a serial homology between this plate and those of the arm joints; to compare it, for instance, with a consolidated dorsal, two laterals,* and possibly a ventral; to find, in other words, that the portion of the ray in which they lie is a true arm division or "joint." My attempts, however, have not been rewarded with great success, and it seems more probable that they are not comparable with other arm plates. Students of Crinoid morphology do not find the homologues of terminals in this group, and there is evidence that they

* Sladen says (*op. cit.*, p. 30): "The comparatively large size of the terminal plate at an early stage of the young Asterid is due, in my opinion, to a coalescence of primitive lateral plates with the primitive, or first formed, rudiment of the terminal, — a circumstance which further strengthens my view of the secondary character of the terminal plate." It would, however, seem from the growth of the plate that such a coalescence does not take place, or at all events I was unable to observe it. It is suggested that the absence of lateral plates (marginals?) allows the sides of the terminals to grow into their places.

are not homologous with the oculars of the Urchin. Whether there are plates in the young urchins which are homologous with the terminals of the starfishes is a question upon which more knowledge of the development of the calcareous plates of the Echinoids may throw some light.

According to Ludwig (p. 188),* A. Agassiz "halt die jungen Terminalia für die Dorsalschilder des Erstgebildeten Armgliedes, eine Bezeihung die ebenfalls nicht korrekt genau ist." Agassiz says, "The only calcareous deposits we have ($y\ y^1$, fig. 32) are evidently parts of the first arm joints, the dorsal (y, fig. 32), and the side arm shields (y^1, fig. 32) of that joint, which consist at present of but a few rods indicating their future position." (Embryology of Echinoderms, p. 20.) This was written of an Ophiuran with a pluteus, which is probably Ophiopholis. Agassiz uses the term "arm joint" elsewhere in his paper to designate one portion or section of the arm. I am unable to understand exactly what Ludwig means by the above criticism of Agassiz, unless it is that the terminals (dorsal shields, Ag.) do not belong to the first formed arm joint, or possibly that the terminals do not indicate an arm joint. One of these interpretations is the best I can make of his meaning. If we consider an arm joint among the Ophiurans to mean a portion of the arm with a dorsal, two laterals, and a ventral with enclosed organs, the portion of the ray in which the terminal lies might not be called an arm joint, since separate calcifications for lateral and ventral plates do not exist. However the terminal may be homologized, it originates like a dorsal, and grows around the terminal tentacle forming laterals and ventral. In the structure of the plates, as in position and time of origin, it differs from all other dorsals, and consequently morphologically may be held by some not to be an arm joint, or to belong to the first formed arm joint. Possibly that may be the meaning of Ludwig's criticism above quoted. If not, I have been unable to see the force of his criticism.

In speaking of an early stage of Asterina in which the first dorsals, or "radials," are formed, Sladen† says: "The first formed plates in the viviparous or abbreviated larva are the primitive elements of the terminal plates, the basal plates, and the dorsocentral plate. These become well developed before any traces of the radial plates make their appearance. Concurrent with the radial plates the lateral plates (interambulacral plates) are developed." He might have added also certain mouth plates, ambulacrals, and interambulacrals (adambulacrals).

* Entwicklungsgeschichte der *Asterina gibbosa*, Forbes.

† Sladen, *op. cit.*, p. 31, fig. 15.

Primary Radials. — The first radials of a Crinoid, according to Sladen, are represented by the Intermediare in Asterina.* There is but one set of plates which can be compared with the Amphiura primary radials, and these are the first of the dorsal plates of the arms. Notwithstanding the fact that these plates have a different time of origin† as regards the genitals, Sladen regards it possible that they may be called the primary radials.

If we accept these plates as homologues of the primary radials, they must be regarded as very much belated in time of formation. Inside the radials of the disk of Asterias are representatives of the under-basals and similar radial plates.

Connectives. — The homologies of the numerous small plates and bars by which the primary plates on the abactinal hemisome of the body are joined together were not identified with definite plates in the Am-

* Although it can readily be granted that the first dorsals occupy the same relative position as the radials in Amphiura, it is a question whether we are justified in carrying our comparisons so far as to homologize them. I grant that their position on the radius is the same, and that retardation in the time of appearance of plates has very little importance morphologically ; but it must be remembered that we are attempting to homologize plates in stages where we know there are unrepresented plates *inter se* in stages where there are plates in the starfish which cannot be referred to those of Crinoids, and plates in the Crinoid which have, as far as we know, no representatives in the starfish.

† While it is generally true that in Ophiurans the radialia appear before the "basals," in one case, according to P. Herbert Carpenter (On the Apical System of Ophiurids, p. 8), basals are formed on the disk where no radialia are represented (*Ophiomitra exigua*, Lyman). It would seem improbable that in this instance radialia had formed and been absorbed. Carpenter (Notes on Echinoderm Morphology, No. XI.) says of the radialia, "They appear before the basals in the Ophiurids, but after them in other groups." I confess surprise at this statement, especially as three years before he had himself pointed out that *Ophiomitra exigua* "has no radials at all, nothing but the five interradial basals (3) intervening between the dorsocentral (1) and the radial shields," and I can only explain it on the supposition that he believed that radials had formed and disappeared, that they are formed later, or that he had changed his mind on the subject.

Carpenter's criticism of my use of "abaxial basals" I will not consider here; but as I nowhere in my paper use the combination "adaxial interradials," I fail to see why he should speak of any plates as my adaxial interradials ("his adaxial interradials").

Carpenter's statement (*op. cit.*, p. 313, lines 12–17) that every previous writer regards basals and interradials as fundamentally distinct, seems to have been written without remembering the fact that Sladen in considering certain starfishes (*op. cit.*, p. 33, lines 27, 29) uses interradial for basal, and to explain what he means by interradials uses the following combination: "interradials (i. e. basals)."

phiura. Undoubtedly a few of the larger might be compared, but, as the connectives are not primary plates, they vary very greatly in number among different genera of starfishes. Moreover, they appear late in development, even after generic features are acquired. A notice of their modification is made under my comparison of Asterias with other starfishes. Not enough is at present known of the smaller plates of Amphiura to attempt any comparison of them with the connectives of Asterias.

Oral Ambulacrals. — The oral ambulacrals early take the form of the "spoon-shaped" plates of Amphiura. In their early condition they approach more nearly the form of the ambulacrals of Amphiura than any of the ambulacral rafters of Asterias, which leads me to think that they are really ambulacral in their nature. As growth goes on, the oral ambulacrals lose their resemblance to the spoon-shaped plates, and resemble more closely those interambulacral plates which later appear in the starfish arm. The early resemblances which have led me to regard the oral ambulacrals as the same as the "spoon-shaped plates" are: 1. Their position and number. 2. Their elongation in early stages parallel with the water tube. 3. Their time of formation. The only one of these three reasons which lacks observation is the third. While we know that in Asterias the first plates of the actinal region to form are the circumoral ambulacrals, we do not yet know this for the spoon-shaped plates of Amphiura. I believe that they are the first, but cannot as yet definitely state this to be a fact.

The later resemblance to interambulacral plates is caused by their growth to the interradial regions and the presence of spines. Notwithstanding this resemblance to adambulacral plates of the oral ambulacrals in the interradii, Asterias is classified as a starfish with an ambulacral mouth. In starfishes in which the interambulacrals enter into the formation of the mouth as well as the ambulacral, it may be supposed that the growth of the adambulacrals of the mouth has prevented the ambulacral from pushing into the interradii. These are possibly intermediate, as far as the mouth goes, between Asterias and Amphiura. In Amphiura the oral ambulacrals, even in late stages, are kept in the condition of spoon-shaped plates similar in relative position to the water tube to embryonic ambulacral orals of Asterias. The retention of a biserial arrangement of the feet in Asteroids with adambulacral mouths may be correlated with the growth of the adambulacrals in early stages. Like the structure of the mouth parts, the rows of legs are biserial, as in Ophiuroids.

Interbrachial Ends of the Oral Ambulacrals. — The interbrachial ends of the oral ambulacrals in the starfish are represented in Amphiura by two separate plates, known as the first and second pair of adambulacrals. While in Amphiura these plates arise from two separate centres of calcification on each side of the arm (twenty centres in all), and in Asterias they appear to arise directly from the ambulacrals of the oral region as a single interbrachial (ten in all), their position and their relation to the mouth lead me to suppose that they are really the same. From the existence of a pair of spines on each oral adambulacral it is necessary to suppose that two plates are consolidated in early stages in Asterias. The greatest difficulty which has been encountered in supposing the homology which I have indicated as a correct one is the fact of origin from different centres of calcification in the one case, and from the ambulacrals in the other (Asterias). I am forced to admit from my study of my preparations that it looks as if the account which is given above of the origin of the oral adambulacrals from the ambulacrals (oral) is correct, although an error may have crept in in this observation. I have no doubt that the adambulacral is single (ten in all rays) from the beginning. The existence of the spines in twos leads me to look upon each oral adambulacral as a compound structure.

First Interbrachial. — The homologue of this plate of Asterias in Amphiura is one of the most difficult problems connected with the whole subject of the morphology of the plates of Echinoderms. It is a most difficult problem to determine what plates in Amphiura correspond with these plates in Asterias. The term odontophore, as others have already shown, is poorly chosen to designate these plates, but as the term has received a signification which is difficult to denote in any other way at present, it is here retained.

The plates which I have identified as odontophores bear the same relation to the oral plates as the so called orals in Amphiura. They do not, however, have a similar origin in the two.

In Amphiura the orals originate on the border of the abactinal hemisome, and gradually grow down on the actinal side until they come to occupy a position relatively the same to the adambulacral as the odontophores to the oral adambulacrals. One of these, according to Ludwig, is a madreporite.

In Brisinga, according to Perrier, the madreporite is situated on one of the odontophores. It would seem, therefore, a just conclusion, that the odontophores and orals are homologous.

If, however, we accept the theory that the orals are homologous with

the odontophores, we certainly cannot also believe that the genitals of the starfish, interradials of which the madreporic body may be one, are also homologous with orals. There is a manifest impossibility that orals can be the same as genitals, and odontophores at the same time. There must be some mistake somewhere if they are compared to both.

If we examine the observations in regard to the fate of the primary interradial plates (orals) in Amphiura as recorded, proof seems to be wanting in observation that they do form the orals. We may readily concede that the madreporic plate may form interradially, and that it may grow down and form an oral, but is it not a leap at a conclusion that the other plates in other interradii do the same thing? Can we not suppose, then, that the madreporic plate is morphologically different from so called genital plates? Are we forced to place it in the same category as other genitals? It seems to me that at present we may say that it is possible that the madreporic plate of Asterias is a modified homologue of an odontophore which has become consolidated through the stone canal with a genital, and that it is the same as that of the oral Amphiura. The orals of Amphiura are, then, the same as the odontophores of starfishes.*

Dorsals. — The dorsals of Asterias are thought to be homologous with the dorsals of Amphiura.† They originate in the same relative position, have the same sequence in development, and to all appearances are identical. While in Asterias they bear spines and in Amphiura are destitute of these structures, this fact does not seem of great importance in showing a want of homology of the two. As the Asterias matures, the relative predominance in size as compared with other plates is diminished, while in Amphiura it is increased. It is thus brought about that in the older stages of Asterias it is more difficult to recognize the dorsal plates. This results both from the relatively small development of the dorsals and the appearance of dorsolaterals and connectives, neither of which are thought to be represented in Amphiura.

* The mode of growth of the odontophore of Brisinga, as recorded by Perrier, seems to differ from that of Asterias, — a fact which does not seem surprising considering the other important differences in the two genera. My observations on Asterias support Sladen and others, that the odontophores are formed on the actinal hemisome.

† The dorsals in the young Amphiura were first figured in my paper on the development of the calcareous plates of Amphiura (Pl. III. fig. 19). They are not represented in any of Ludwig's figures, although I believe that they will later be found in stages younger than his fig. 21, as already pointed out.

Ventrals. — No plates corresponding with the ventrals of the Amphiura were found in the young Asterias which were studied. In my account of the development of the plates of Amphiura some difficulty was found in a comparison of the way in which the ventrals develop with the way the "embryonic median row of plates" corresponding with these were formed in Asteracanthion according to A. Agassiz. I was at that time anxious to study the embryonic ventral plates of Asterias, and when opportunity occurred took up the subject for this purpose. I was disappointed, however, for if embryonic ventral plates do exist in some starfishes other genera must be studied. I found no trace of them in any of my young larvæ of Asterias.*

The ventrals of Amphiura are believed not to be represented in Asterias. I have already elsewhere adduced evidence which is thought to be conclusive, as far as mode of formation goes, that the ventrals of Amphiura are not homologous with the embryonic plate of the middle actinal line of the starfish ray as described by Agassiz. My argument then was that the ventrals in Amphiura are *unpaired median* † calcareous deposits, while the theory would imply that the so called embryonic plates of the starfish were formed by a coalescence from two calcifications, one on each side (see Agassiz, *op. cit.*, p. 91). As I am unable to recognize in Asterias the middle actinal row of embryonic spines, it is not possible for me to find in Asterias homologues of the ventral plates of Amphiura.

Interambulacrals. — The interambulacrals of the starfish (Amphiura) are recognized by some authors in the laterals, while others consider that

* It is, of course, possible that the species of Asterias which I studied may not be the same as that in which the median actinal "embryonic plates" have been described. The difference in the colors of the females, already mentioned, would seem another fact pointing to such a conclusion.

† This fact is pointed out by Ludwig, and in the light of his studies it is probable that the figure of Schultze (fig. 6) represents a ventral in the median line of the under side of each arm. According to Ludwig, the erroneous idea that the ventrals are originally paired structures has been reproduced by Carpenter (Oral and Apical Systems of the Echinoderms, Part II., Journ. Micros. Science, Vol. XIX. p. 21) and Semper (Reisen im Archipel der Philippen, II. Holothurien, 1868, p. 162). Ludwig says that, to show the homology of the ventral plate of Ophiurans with the adambulacral of the starfish Semper instances the fossil *Protaster Sedgwickii*, Forbes, as an Ophiuran with paired ventrals. Semper saw the difficulty of comparison of the *unpaired* ventral of most Ophiurans with *paired* adambulacrals of starfishes. It seems to me that Ludwig meets the case of Protaster exactly when he says, "Leider ist nun aber Protaster ein noch so ungenügend bekanntes Fossil dass man dasselbe überhaupt als Beweismittel in dieser Sache nicht gelten lassen kann."

the Ophiurans have no interambulacrals (adambulacrals). In my paper on Amphiura the laterals were regarded as adambulacrals, following Ludwig and P. Herbert Carpenter. I am not, however, sure that they are not rather the marginals, and that Agassiz is right in considering that there are no interambulacrals in Ophiurans. The early form and growth of the marginals on the border of the arm in both Asterias and Amphiura is similar. The interambulacrals in starfishes (Asterias) never approach in form the laterals of Amphiura. In genera allied to the Ophiurans, Astropecten, etc., the marginal plates get ophiuroid in nature, and resemble the lateral plates of the young Amphiura. In certain deep-sea genera of starfishes there is a resemblance between the marginal plates and the lateral plates of some Ophiurans when dorsals are not developed. In the light of these facts I must register my doubt whether I am right in following those who regard the lateral plates of Amphiura as adambulacral, homologous with the interambulacral (adambulacral) of the starfish. It looks as if true adambulacrals were yet to be made out in Amphiura. The resemblance of the marginal plates of the young starfish to the marginal plates of Zoroaster is still another embryonic feature of deep-water Asteroids.

The following summary may be made of the preceding observations: —

1. The first plates to originate in the young starfish are the terminals. These plates are simple (not formed by a coalescence of more than one calcification). They form a protecting cap, shielding the newly formed ambulacrals, interambulacrals, and possibly marginals.

2. The genitals originate *after* the terminals. The genital which lies contiguous to the madreporic opening does not always antedate in time or excel in size other genitals. It grows around the madreporic body, or end of the madreporic tube.

3. The madreporic body, madreporite, is a late formation (after the rudiments of the stone canal).

4. The dorsocentral originates after the terminals and genitals, *before* any plates on the actinal hemisome.

5. The first plates to form in the body after the genitals have a radial position in a circle inside the genitals. The second circle is also radial, and lies inside the circle of the first body, or somatic radials. A third and inner circle appears before the interradial somatic plate.

6. The first plate in the circle outside that of the genitals is the first dorsal of the arms. This plate ("Radial," Sladen), when the

arm of the young starfish is broken from the body, always remains on the arm.

7. The dorsals, or median *row* of plates on the dorsal surface of the arm, originate peripherally to the first dorsal ("radial"), and are at first relatively very large.

8. The dorsolaterals do not appear in the same sequence as the dorsal. (The oldest dorsolaterals may not be the nearest to the body.)

9. Marginals appear after ambulacrals and before (of this there is some doubt) interambulacrals (adambulacrals).

9. Oral ambulacrals are the first plates to form on the actinal hemisome. When they first appear there are the following calcifications on the abactinal hemisome: 1st. 5 terminals; 2d. 5 genitals; 3d. 1 dorsocentral; 4th. 30 spines on terminals.

10. The oral ambulacrals are at first parallel with the radial *culs-de-sac* of the water system. By subsequent growth they are placed at right angles to the same. They are at first ten in number.

11. The interbrachial ends of the oral ambulacrals of adjacent radii (arms) grow towards each other, forming two parallel ends in each interradius, of which each bears two spines. The median end of each oral ambulacral bifurcates into a dorsal and ventral part.

12. All other ambulacrals, with the exception of the oral, originate with axes at right angles to line of radii. They form near the middle line of the under side of the ray, and grow towards the peripheral. The adoral are the first formed. They bifurcate in the neighborhood of the median line.

13. The first interambulacrals (adambulacrals) form after the corresponding ambulacrals in the interval between the marginal ends of successive pairs of the same. Their centre of ossification is from the first different from that of the ambulacrals.

14. Marginals form before (?) interambulacrals (adambulacrals).

15. The first interbrachials (odontophores) originate as heart-shaped, interradially placed calcifications, five in number, each abactinally placed to the interbrachial ends of the oral ambulacrals. In one specimen four of these were first observed; that which lies in the same interradius as the madreporic tube was retarded in growth. The first formed interbrachials are not wholly concealed from view, as in deep-sea Asteroids. When the first interbrachials (odontophores) form, the following plates have begun to appear? 1st. 5 terminals; 2d. 5 genitals; 3d. 1 dorsocentral; 4th. 10 oral ambulacrals; 5th. 20 ambulacrals.

16. No ventral embryonic row of spines or plates was observed in the genus and species studied.

17. Genitals of Asterias are thought to be homologous with "basals" of Amphiura.

18. First interbrachial (odontophore) is homologous with the orals of Amphiura.

19. Madreporic opening is placed on two homologically different plates in Asterias and Amphiura.

20. 1st. Genitals; 2d. Dorsocentral; 3d. Dorsals; 4th. Interambulacrals; 5th. Terminals; — represented in Amphiura by, 1st. Basals; 2d. Dorsocentral; 3d. Dorsals; 4th. Laterals; 5th. Terminals. (Homologous plates numbered the same.)

21. Oral ambulacrals of Asterias are represented by the "spoon-shaped plates" of Amphiura.

22. "First and second adambulacrals" of Amphiura have no homologue in the mouth parts of Asterias.

23. Ventrals of Amphiura are not represented in Asterias.

24. Dorsolaterals and connectives of the arms were unrecognized in Amphiura. The homology of the marginals is in doubt, and it is probably not represented in Amphiura. Possibly the marginals are homologous with the (adambulacrals) laterals.

Cambridge, January, 1888.

EXPLANATION OF THE PLATES.

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a. Blastopore.
ad. Interambulacrals.
ad^1, ad^2, ad^3, ad^4, ad^5. Interambulacrals in sequence.
am. Oral ambulacrals.
am^1, am^2, am^3, am^4, am^5. Ambulacral rafters in sequence.
amd. Interambulacral ends of the oral ambulacrals.
bn. Brachiolarian notch.
c. Connectives.
cbw. Circular blood-vessel.
cw. Circular water tube.
d^1. First dorsal (radial).
d^2, d^3, d^4, d^5, d^6, d^7. Dorsals.
dc. Dorsocentral.
dd^1, dd^2, dd^3. Early formed body plates in radial lines.
dl. Dorsolateral, or lateral dorsal.
f. Feet.
g, g^1, g^2, g^3, g^4, g^5. Genitals (basals).
g^1. Genital near the madreporic opening, through which the madreporic tube opens.
i. Intestine.
ib. First interbrachial, or odontophore.
ib^2 Second interbrachial.
ibn. Interbrachial notch.
lt. Lateral region of the terminal.
m, m^1, m^2, m^3. Marginals.
mb. Madreporic body.
mt. Madreporic tube
o. Mouth.
œ. Œsophagus.
om. Oral ambulacrals.
pd. Pedicellaria.
sp. Spines.
st. Stomach.
stc. Stone canal.
t, t^1, t^2, t^3, t^4, t^5. Terminals.
t, *ta.* Terminal tentacle, or extremity of the medial water tube.
ub. Unabsorbed region of the brachiolaria.

In Plate I. Fig. 1, t^4, t^5, g^2, g, and g^4 are seen through the stomach of the brachiolaria; gt^1 and t^2, g^1 and g^5, lie on the same side of the brachiolaria as the observer; g^2 and g^5 are seen in profile, and lie on the lower surface.

In the figures where the ambulacrals are represented, they are made very much darker than in nature, in order to illustrate diagramatically their relationship to the other plates. All the figures were drawn with the camera lucida, reduced in size in lithography. Where a single arm only is represented, it is to be remembered that the unrepresented arms are in the same condition of development.

PLATE I.

Fig. 1. View of the posterior (anal) extremity of the body of a brachiolaria of Asterias, showing the first appearance of the calcifications which ultimately form the terminals and genitals. The greater part of the brachiolaria is not shown in this figure.

Fig. 2. A somewhat older brachiolaria, in which the brachiolarian arms are beginning to be absorbed. The dorsocentral (*dc*) has just appeared. The specimen from which this was drawn was no longer free-swimming, but was taken with a pipette from the bottom of the jar in which the starfishes were raised. (Abactinal view.)

Fig. 3. A somewhat older starfish in which the brachiolarian arms are still more reduced in size by absorption. (Abactinal view.) In this stage the radial canals are seen through the body of the starfish, and the ambulacrals have just begun to appear.

Fig. 4. The same, slightly younger than the last. This figure shows the plates only; the soft parts, with the exception of the brachiolarian arms, are not represented.

Fig. 5. Lateral view of a brachiolarian younger than Fig. 4, showing position of the anus, *a*, and the madreporic body, *mb*. The lower part only of the brachiolarian is shown.

Fig. 6. Side view of a somewhat older starfish separated from its brachiolaria, showing the relation of the madreporic body to the first genital, *g*.

PLATE II.

Fig. 1. View of a young starfish, from the abactinal side, in which the brachiolarian arms are almost wholly absorbed, and the interbrachial notches have appeared. The body of the starfish and of the brachiolaria is seen through the walls of the animal.

Fig. 1^a. Two rudimentary spines of the terminals in their primary form. The part represented is one of the interbrachial notches.

Fig. 2. A somewhat older starfish, seen from the actinal side, showing the mouth, stomach, radial tubes, and plates with spines.

Fig. 3. Young starfish, seen from the actinal surface, with the first ambulacrals, oral ambulacral, *am*, well formed. The second pair of ambulacral rafters, am^1, are just beginning to appear.

Fig. 4. An older starfish, seen from the actinal side, showing the arrangement of the plates. The soft parts in this and the former figure have been removed. Spines are removed from most of the terminals, and appear on one arm only.

PLATE III.

Fig. 1. Single arm of a starfish somewhat older than Pl. II. Fig. 4. View from the actinal side. Three ambulacral rafters have appeared. The youngest, am^2, is very small.

Fig. 2. Somewhat older starfish, in which four ambulacral rafters have formed, and in which the interambulacrals have begun to develop. View of one arm from the actinal region. The specimen is slightly older than Pl. III. Fig. 1.

Fig. 3. View of the tip of the arm of a somewhat older starfish, showing the terminals and the ambulacrals just forming under the protection of the terminal. The ends of the spines are not represented.

Fig. 4. View of the arm and the plates of the body of a somewhat older starfish than Fig. 2. Seen from the actinal side. The outlines only of the plates of the body are represented.

PLATE IV.

Fig. 1. Abactinal view of an arm of a starfish a little older than Pl. III. Fig. 1, showing dorsocentral, two genitals, the first of the medial dorsal line of plates, and the terminal with its spines. Ambulacral plates in this and in Fig. 2 shown through the abactinal system.

Fig. 2. Abactinal view of an arm of a starfish older than Fig. 1. Portions of two genitals, the marginals, dorsals, and a terminal, are represented.

Fig. 3. View of a starfish from the abactinal region. From a specimen somewhat older than that shown in Fig. 2. Four of the arms have the plates shown in outline only. The plates of a single arm are shaded, and the spines are represented.

Fig. 4. View of a single arm and the plates of the body of a starfish much older than the last. Seen from the abactinal side. Soft parts have been removed. Spines not represented on genitals and first dorsals.

PLATE V.

Fig. 1. View of the genital and first dorsal (radial) plates of the body of a young starfish, of about the same age as Pl. IV. Fig. 1. All the plates of the arms removed.

Fig. 2. The same somewhat older, showing the first formation of the plates, dd^1, between the ring of genitals and the dorsocentral.

Fig. 3. Still older starfish, showing the body plates between the ring of genitals and the dorsocentral. View from the abactinal region. The radial lines are from d^1 to dc.

Fig. 4. Much older starfish, showing the network of plates which compose the abactinal surface of the body. These plates are from a starfish almost an inch in diameter (from tip of one arm to another).

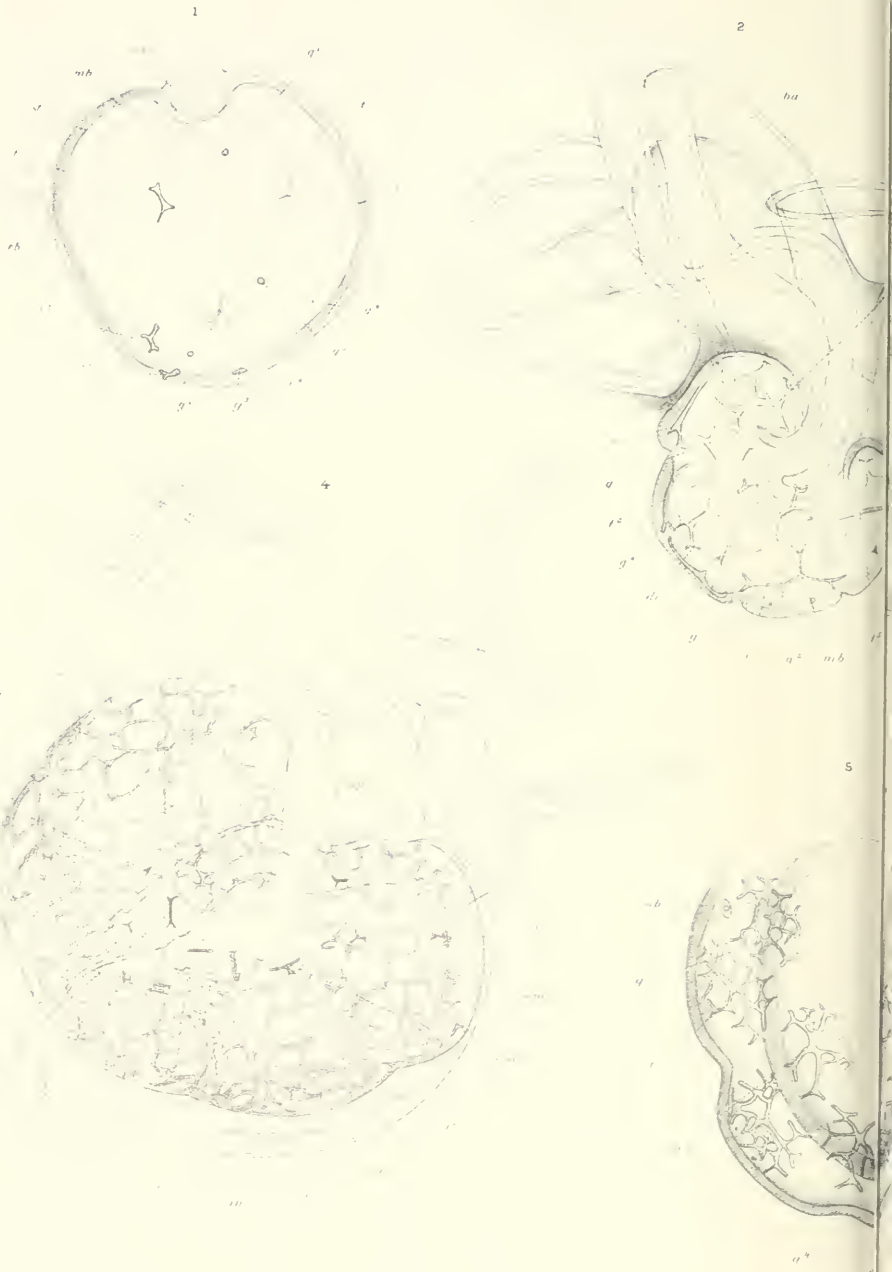
Fig. 5. Enlarged view of the interbrachial region of a young starfish. The odontophore, *ib*, appears as a heart-shaped plate in the angle of the ray. Actinal view. Same age as Plate II. Fig. 1.

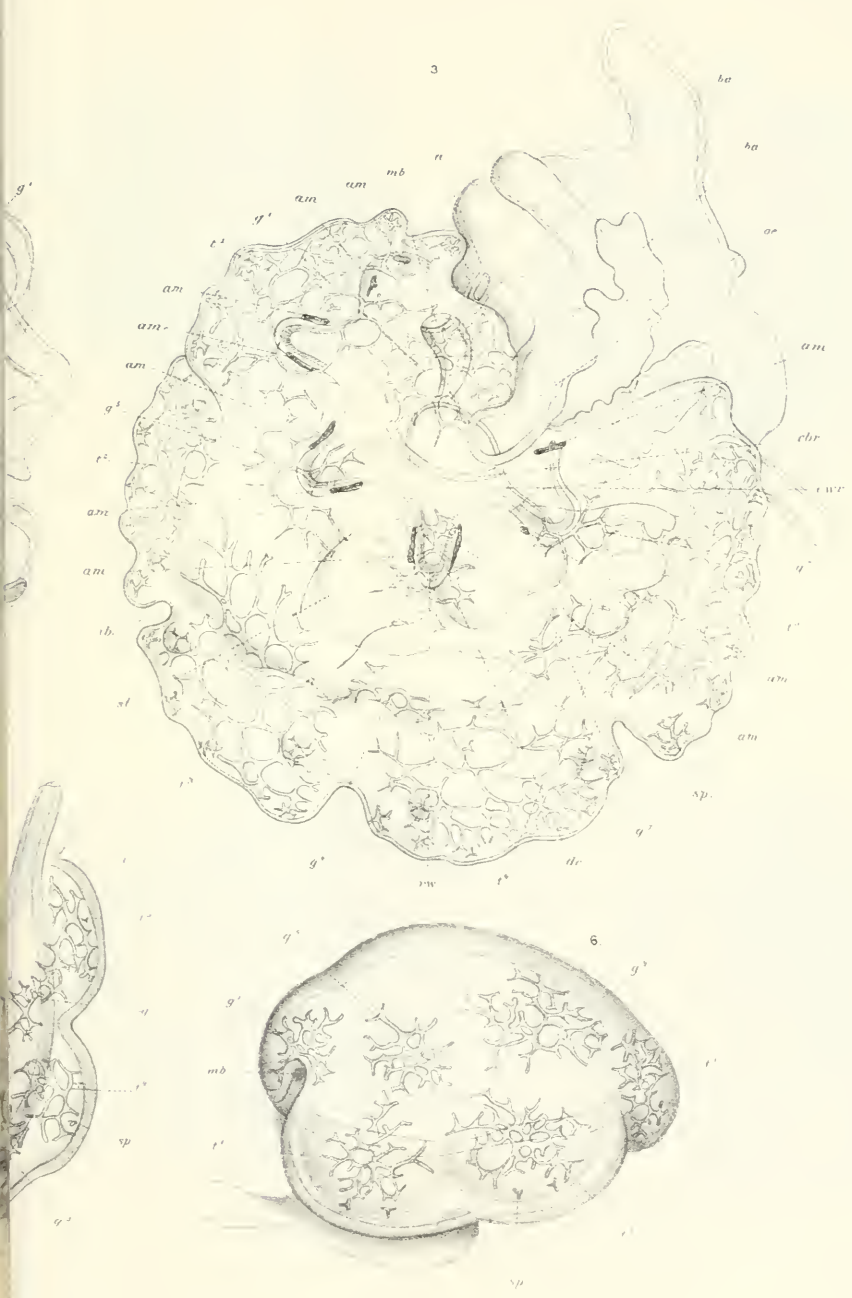
Fig. 6. The same, somewhat older. Actinal view.

Fig. 7. Still older view of the same.

Fig. 8. View of an older stage, in which a second interbrachial, ib^2, has formed.

The shaded plates of Figs. 5, 6, 7, and 8 are oral ambulacrals and ambulacral rafters. The two crescentic plates, unshaded, in the upper part of Fig. 5, are the edges of the terminals, not marginals, *m*, of Figs. 6, 7, and 8.

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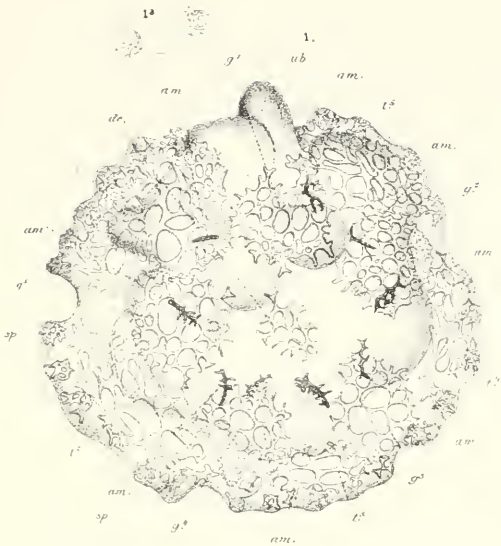
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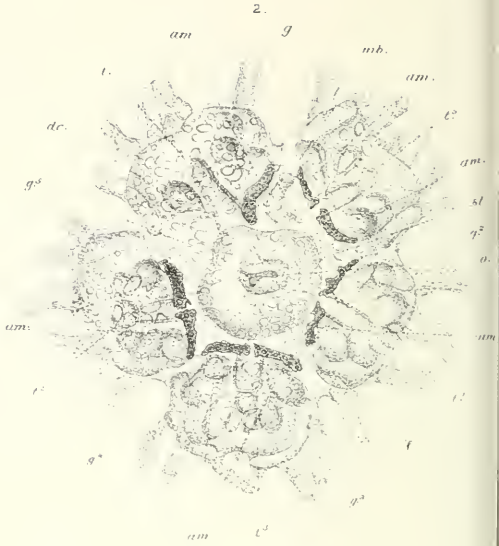
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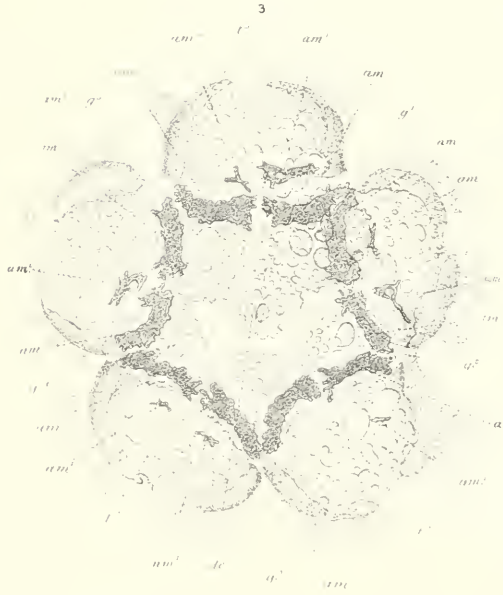
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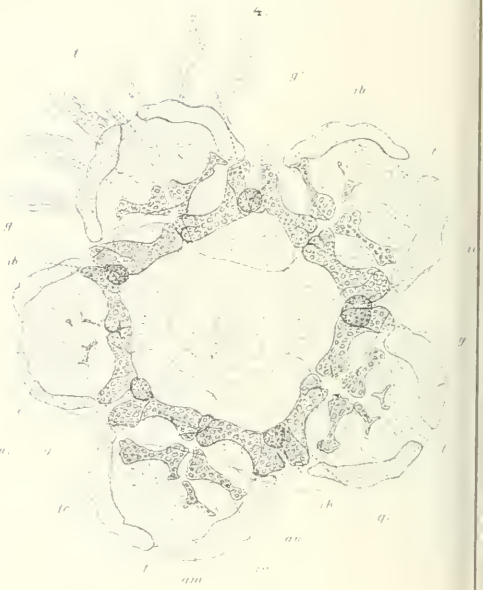
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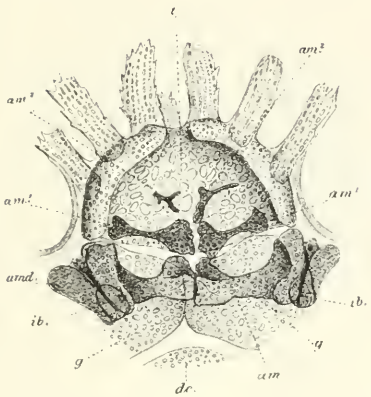
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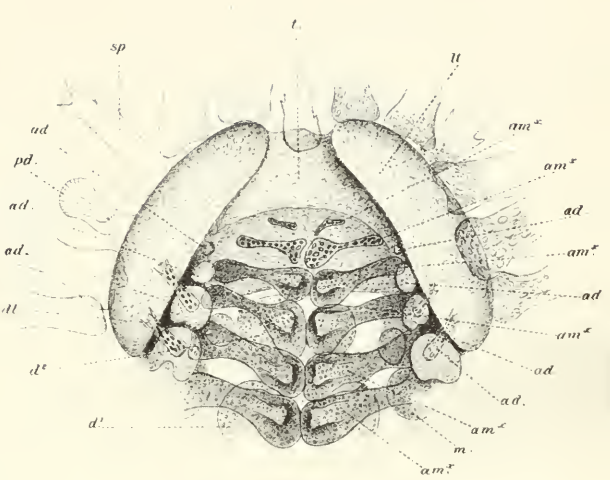
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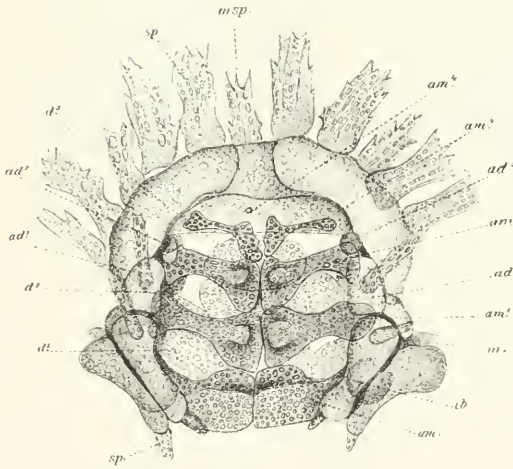
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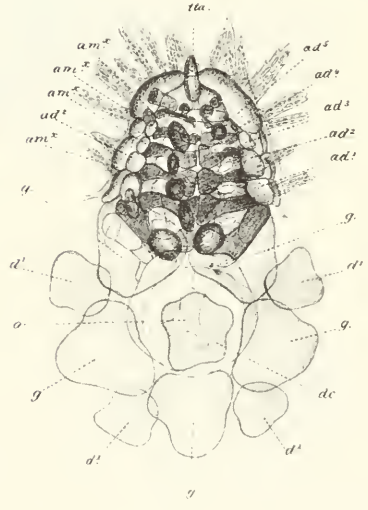
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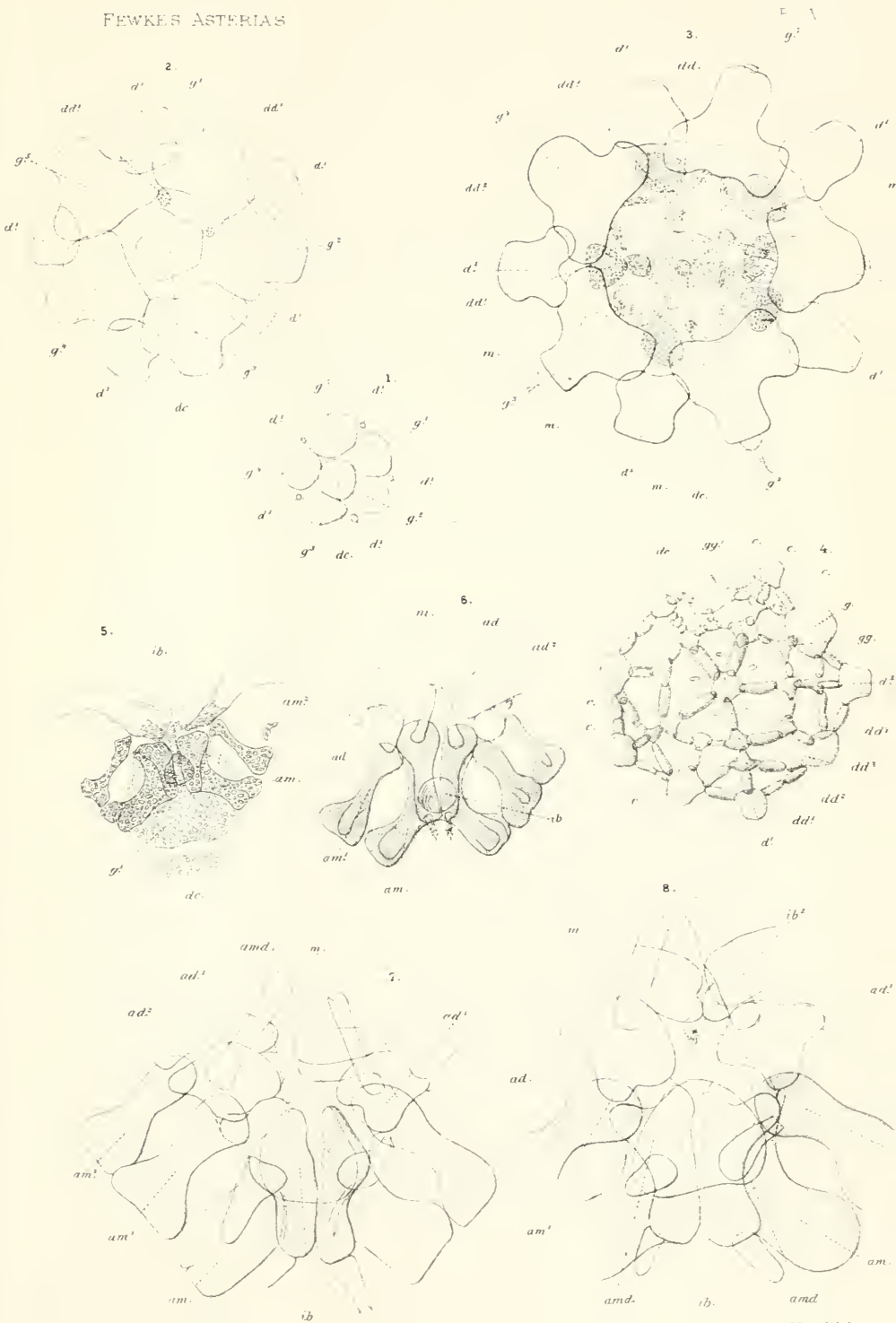
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No. 2. — *On the Lateral Canal System of the Selachia and Holocephala.* By Samuel Garman.

Soon after his return from the Hassler Expedition, in 1872, Professor L. Agassiz placed before me, his pupil at the time, a specimen of one of the Batoidei, with the remark, "See what you can find out about it." A preparation of the lateral line system was one of the results. This was followed, under Professor Agassiz's directions, by other preparations of the same system, which, one after another, were handed over to the artist of the Museum to be figured. The work was continued thus for more than a year, without my knowledge of the fact that Dr. B. G. Wilder had previously been engaged on similar work while assistant of Professor Agassiz. And it was not until about 1883 that the Director of the Museum desired me to prepare for publication my own material, and that accumulated under Professor Agassiz's directions. It was found that, in order to use the manuscript left by Dr. Wilder, many changes would be necessary, and it was thought better on the whole not to attempt to incorporate it with my own. Dr. Wilder's dissections have been used as far as possible in the descriptions. They were figured by Mr. Roetter, and included a representative of each of the following genera: Scoliodon, Prionodon, Mustelus, Triacis, Isurus, Odontaspis, Alopias, Ginglymostoma, Scylliorhinus, Heterodontus, Acanthias, Rhina, Pristiophorus, Pristis, Raia (*R. lævis*), Dasybatus (*D. tuberculatus*), Pteroplatea (*P. valenciennii*), Myliobatis (*M. freminvillei* and *M. aquila*), Aëtobatus, and Rhinoptera (*R. brasiliensis* and *R. jussieui*). In addition to these there were preparations of several types of which no use has been made, as they had been duplicated in my own work. Chimæra and Callorhynchus required no dissection; a drawing of the latter had been made by Mr. Roetter. The figures by this artist were made to be lithographed, and were not at all suited to the engraver's process, by which this publication was to be illustrated. Consequently outlines have been used instead of his drawings.

This leaves me responsible for all the text, and for the dissections and sketches of Dicerobatus, Pteroplatea (*P. hirundo* and *P. marmorata*), Dasybatus (*D. nudus* and *D. dipterurus*), Tæniura, Urolophus, Discens,

Potamotrygon, Narcine, Torpedo (*T. californica* and *T. marmorata*), Raia (*R. ocellata*), Uraptera, Syrrhina, Rhinobatus, Somniosus, Chlamydoselachus, Heptabranchias, and Cestracion (Zygæna); also for sketches of Chimæra, Callorhynchus, and Pristiophorus; and for the outlines and sketches of such as had been drawn by Mr. Roetter.

With a few exceptions the names of the canals are those adopted by Professor Agassiz.

The structures to which attention is here directed are those on the Selachia and Holocephala, which correspond to the lateral lines of the Fishes. On the individual they form a system of branching canals, or tubes, tubules, and branchlets, which has received a variety of names at the hands of different writers: slime canal, mucous tube, water canal, lateral line, etc. To avoid confusing with the unbranched hyaline mucous ducts of the ampullæ of Lorenzini, the term canal will in this paper be applied exclusively to the organs comprised in the system under discussion. The manner in which the tubes branch and connect, and the fact that they are sometimes represented by mere furrows in the skin, make this designation the more appropriate. In addition, since it has been pretty well established that their function is that of very delicate tactile organs, receiving and carrying the slighter vibrations of the water, noting changes of density, currents, etc., a special name, Tremognosters, to be applied to these particular canals, distinguishing them from the many other canals of the body, is introduced as likely to prove still more convenient.

These canals, or tubes, lie in or under the skin on both body and head. They open externally either as furrows or by means of pores, that in some cases enter the tubes directly and in others are approached by tubules. The inner layers of their walls are furnished with series of nerve-endings, which, as also the external openings of tubular canals, are segmentally arranged. In different parts, the structure of the walls varies from fibro-cartilaginous, on the top and sides of the skull, to very delicate transparent tissue, under the snout. Granulation, apparently resulting from calcification, occurs in the cephalic tubes of certain genera. There are no glandular attachments; the vessels are simply canals, open at each end, and more or less so along their sides. On the head they are innervated mainly from the fifth pair, and on the body by a branch of the vagus, the nervus lateralis.

The development of the system, as worked out by Balfour in Scyllium, coincides closely with that of the Teleostei. According to Beard the lateral line in the embryo salmon first appears opposite the hyoid arch,

a little behind the ear capsule, on the level of the notochord; and it is formed by the splitting off of some of the cells of the inner layer of the epiblast. From its point of origin, where it is broadest, it grows backwards along the body. This cord of cells, as Beard calls it, is no doubt what Balfour describes, in Scyllium, as a linear thickening of the mucous layer of the epidermis, or as a linear streak of modified epidermis. This linear sense streak is in Balfour's opinion the primitive structure from which the various forms of the line have originated. He says, further, that the thickened streak becomes a canal in Scyllium, not by the folding over of the sides, as in Teleostei, but by the formation of a cavity between the epidermic and the mucous layers of the epiblast, and the subsequent enclosure of this cavity by the modified cells of the mucous layer of the epiblast constituting the lateral line. The cavity appeared first at the hinder end of the organ, and thence extended forwards. After formation the canal gradually recedes from the surface, retaining its connection, however, at a series of points corresponding to the segments, points at which the segmental openings are afterward formed. As compared with the open canal on Chimæra, the tubular canal is a secondary form. In regard to the innervation on the trunk by the lateral branch of the vagus, the nerve was found to originate as the other nerves, and, pushing its way backward, to follow the course of the lateral line. Originally the line is supposed to have been restricted to the anterior part of the body, and thence, extending farther and farther backward, it carried with it the lateral branch of the vagus, until ultimately the latter was prolonged far beyond the position it originally occupied. Beard says of this nerve, in Salmo, that it originates far from the epiblast and growing backward approaches the skin so as to lie between the two muscle plates just below the epiblast, never fusing with the lateral line, but always separated from it by the cuticular basement membrane of the epidermis.

Balfour found the canals of the head and the ducts of the ampullæ to be formed from the mucous layer of the epidermis, very much as the lateral line; but their innervation is effected by simple branches of the fifth and seventh pairs, which reach them in various places without following their courses, unlike the nervus lateralis and the lateral line.

Primarily the openings at the ends and along the sides of the tubes appear to have been in close relationship with the segments of the body, both in regard to position and number. The relations are still apparent in the numbers and in the positions of the tubules at their points of

junction with the main tubes. But in many species, through the descent of the canals below the skin, the consequent elongation of the tubules, and the multitudes of branchlets by which they communicate with the surface, the primary arrangement has come to be greatly obscured. Alopias illustrates this to some extent in the Galei; and in the Batoidei instances are numerous in the Trygonidæ, the Myliobatidæ, the Zygobatidæ, and the Ceratopteridæ.

The tubes contain a thin mucilaginous liquid. This is probably for the most part an excretion, and not an absolute necessity in connection with the function of the system, except, it may be, in so far as it serves the purpose of lubrication. Its retention is hardly possible in the open grooves of various genera, on which the office of the organs is undoubtedly the same. In discussing the purpose of the liquid, one must bear in mind those Teleosts in which the sense bulbs open directly on the epiderm, without either groove or tube, and the likelihood that they represent the primitive condition of the system from which the furrows and the tubular canals have been developed.

Absence of the mucous secretion on the skin of species well provided with canals precludes consideration of the opinion that the object of the latter is to cover the surface with slime.

Series of the follicles in immediate connection with the subrostral canals of certain species lead to the conclusion that the nerve follicles of Savi are really obsolescent tubes of the canal system, in which the section that forms the enclosure or follicle owes its persistence to the presence of the contained nerve. In other words, the follicles represent vanishing and rudimentary tubes. From this it would seem as if Potamotrygon, Disceus, and Urolophus, among others, may be on the way to lose the canals of their ventral surfaces, as has already happened in the cases of Torpedo and Narcine.

The hyaline mucous ducts of the ampullæ are unbranched, have but a single aperture, are closed at the inner end, where entered by the nerve, and are filled by a jelly-like mucous. Plate XXVIII. fig. 1, represents a portion of those of *Raia lævis*, and their distribution as compared with that of the principal canals, fig. 2.

GALEI.

On the Sharks the canal system consists of a vessel on each side of the vertebral axis, extending from the snout to the tail, connected with a similar vessel on the opposite side by a transverse branch near the

occiput, and sending another branch between the eye and the spiracle toward the mouth. Between the lip and the eye, on the lower aspect, the latter branch sends another backward past the angle of the mouth, and, farther on its way forward, sends still another behind each nostril, itself usually joining the main canal at the end of the snout. Commonly a branch from that passing the angle of the jaws extends under the jaw, behind the mouth, toward the middle of the chin; in some cases this branch is disconnected; in others it does not appear; occasionally it is continuous across the symphysis. The branch behind the nostril passes toward a similar one from the opposite side of the head, either uniting with it or approaching it closely for a short distance under the base of the rostral cartilage, after which the two diverge slightly and continue forward to the end of the rostrum. On the top of the skull the tubes are more or less strongly attached to the cartilage, in troughs or depressions in which they are often deeply seated. Under the base of the rostrum there is also a firm attachment to the cartilage. Elsewhere the canals lie at varying depths in the skin or below it. Generally they are tubes with openings to the surface through simple to many-branched tubules. On species of Heptabranchias and on Chlamydoselachus they appear, in great part of their extent, as open dermal grooves. On one of the genera of the Holocephala they are open furrows, on the other they are tubes.

NAMES OF THE CANALS.

Plate I.

The most convenient designations for the different canals, or parts of canals, are those derived from the names of the portions of the body traversed by them, or from those of the organs near which they pass. The propriety of the names *cephalic* for all the canals of the head, and *corporal* for all those of the body, is at once apparent. Their position along the flanks makes the name *laterals* (*l*), by which they are generally known, a very appropriate one for the two main corporals. In the Batoidei there is a canal peculiar to them extending out upon the pectoral fin; this may be called the *pleural* (*p*). On the lower surface it becomes a *subpleural*. The areas enclosed by the pleural tubes are the pleural areas; those sometimes enclosed by scapular tubules on the shoulder are called the scapular areas.

Running longitudinally on the top of the head are the two principal cephalic tubes, the *cranials* (*cr*); anteriorly, on the rostrum they be-

come the *rostrals* (*r*), and after passing below the snout they are known as *subrostrals* (*sr*). At the end of each cranial, on the crown of the head, an *orbital* (*orb*) canal runs outward behind the orbit; below the eye, and below the disk in the flat-bodied Selachians, they become the *suborbitals* (*so*). A transverse tube from one lateral to the other, close to the external openings of the aqueducts, ear openings as commonly named, is the *aural* (*au*). A short *occipital* (*oc*) reaches from the aural to the orbital; or, in other words, from the lateral to the cranial.

On the ventral surface the canal passing lengthwise near each angle of the mouth is the *angular* (*ang*). The portion to which this name is applied is not a long one; farther back on the same tube, the name is supplanted by that of *jugular* (*j*). In some cases these canals are definitely limited by a branch, the *oral* (*o*), putting out transversely behind the mouth; but very often the oral is found to have lost its connection with the other tubes. Rarely the oral is continuous across the symphysis. In front the angular meets either the suborbital or a canal, the *nasal* (*n*), extending behind the nostril, between the latter and the mouth; sometimes the one is met, sometimes the other; whichever it may be, it marks the anterior limit of the angular. The two nasals meet in front of the middle of the mouth, in most cases, and, uniting, form a short *median* (*m*), from which two other tubes, the *prenasals* (*pn*), diverge and run forward to the end of the snout. On a few forms the nasals do not meet. In some instances there is a junction of subrostral and nasal; in others, the subrostral joins the suborbital; in one species the angular and the nasal join, in another it is the angular and the suborbital; but however the junctions may be arranged, a tube of less or more extent lies between the end of the orbital and that of the nasal. Its position is indicated in its name, *orbito-nasal* (*on*).

BATOIDEI.

If one of the round-bodied sharks were to be greatly depressed and flattened, extension taking place on both dorsal and ventral surfaces, the pectoral fin at the same time being expanded and applied to the side of the trunk, the arrangement of the main tubes of the system would be similar to that obtaining on the Batoidei. The subrostral, nasal, prenasal, angular, jugular, and suborbital would appear on the lower surface, as in the Skates and Rays. An important addition to what has been recorded in the Galei occurs in the Batoidei: a *pleural* canal (*pl*), which meets the lateral at the shoulder, runs outward on the pecto-

ral fin, then forward, descending near the head, and, after a backward course of varying extent on the lower surface, unites with the jugular. Or, reversing the direction and starting below, from the jugular, the canal goes out and forward under the pectoral, ascends at the side of the head, then turns out and backward, describing a circuit toward the margins on the top of the fin, and unites with the lateral at the shoulder. Most frequently it is the case that the pleural and the orbital are connected by orbito-pleural tubules; exceptionally these tubes meet directly without the intervention of the tubule. No doubt the pleural originated as a branch of the orbital. Besides this pleural canal on the pectoral, there are usually present several others, post-pleurals, from the scapular curve of the lateral toward the hinder part of the fin, which also are not represented in the Galei. Ordinarily the upper pleurals are abundantly supplied with tubules; sometimes on the lower surface tubules are entirely absent; and on the Torpedoes the ventral portion of the entire system is obsolete. Branches of tubules are generally in pairs; a tubule forks to form a pair; each of this pair forms another pair in similar manner, and so on. This dichotomous branching of the branchlets may be kept up, as in the higher Rays, until on reaching the outer layers of the skin a considerable space is occupied by the mat or rosette formed of the very small tubes and their pore-like openings on each of the tubules. Among the Torpedoes and the Skates the simple unbranched tubule is the common form.

The origin of the pleurals of the Batoids, or the manner in which the group became possessed of these canals, in addition to those possessed by the Galei generally, is a question of considerable interest. Our only clue to the solution of the problem is to be seen in Chlamydoselachus. If the head and body of this shark were depressed, and the pectorals expanded and applied, so as to produce the skate-like form, the spiracular canal would then extend back along the basal cartilages of these fins, they being attached above the gill openings, thus forming the pleural canal, the union of which with the scapular branch of the lateral is only a secondary matter, as shown by the variety in modes of junction, in the Rhinobatidæ, the Raiidæ, and such genera of Trygonidæ as Urolophus and allies. On the lower surface the subpleurals would be supplied by the gular and the canal lying between it and the lip, the oral being limited to the part anterior to their point of meeting. The fact that the additional canals would be acquired in this way, as a necessary consequence of the change of the form, leads, at the least, to a strong presumption that the Batoidei are indebted for their

pleurals and subpleurals to a Galeoid ancestor resembling Chlamydoselachus as far as the possession of spiracular and gular canals is concerned, if not further. And indirectly the tendency of such considerations is to confirm the claim elsewhere advanced that that genus is in great measure to be regarded as a persistent type.

HOLOCEPHALA.

The great differences between Chimæra and Callorhynchus in regard to rostral appendages and claspers, are in reality no greater than those obtaining in their canal systems. Greater divergence than occurs in these genera is not to be seen in the most dissimilar forms of the Sharks. On Chimæra the canals are furrows, as on the body of Chlamydoselachus, and the oral meets the angular; on Callorhynchus the canals are tubes, and angular, oral, and jugular meet the suborbital independently. At the first glance, the differences in the distribution of the cephalic canals in the two genera appear greater than they really are. On comparison, the positions of laterals, aural, occipitals, cranials, and orbitals are found to be similar. In both cases the oral and the jugular cross the median line as series of pores or short grooves, the suborbital extends to the end of the snout, the subrostrals unite under the rostrum to form a median, then separate to meet the nasals, and the nasals are in front of the nostrils, meeting across the middle without forming a median canal or prenasals. It may be added, that in both types the lateral descends, above the lower lobe of the caudal fin, to the lower edge of the muscles, as in certain of the lower Galei.

Affinities with the Sharks, through ancestry, are indicated by the correspondence in laterals, aurals, cranials, orbitals, angulars, and orals. Special points of disagreement are seen in the union of the jugulars, the prenarial location of the nasals, the absence of prenasals, the presence of a median in the subrostrals, and in the connections of the occipitals.

COMPARISONS.

Whether the canal system is a suitable basis for homology and classification, either alone or in connection with other parts of the anatomy, and its importance as such a basis, are to be determined by consideration of the extent of its development and the amount of its variability in the different types included in the class. An exhaustive investigation of the subject would naturally demand a study of the

system in its relations to the general structure and to the habits of the species, and, through the latter, to the surroundings and to their influence upon its evolution and variation. Direct opportunity for much of this is not within reach; but from the material at hand it may be possible to make approximations that at least will be tolerable.

Possession of the organ is quite general; no exception has yet been discovered either in the Selachia or in the Holocephala. A stage of development of the system that is comparatively simple exists on those forms usually called the lower, and on the course from them to the highest the amount of complexity is found to correspond well with the rank as indicated by the brain or other parts of the organization. Between Heptabranchias and Alopias of the Galei, and between Pristis and Dicerobatus of the Batoidei, each step is marked by variation in contour and in the extent and complication of the system of the canals. In the Holocephala a blow is apparently given to the idea that the groove is the lowest, the primitive form of canal, by the fact that Callorhynchus possesses tubes and not furrows like those of Chimæra. This may be no more than an indication that the former is the most differentiated type, the higher in rank. Bony Fishes, also, possess tubes. The fact remains that it is among the lower forms of the Sharks and in Chimæra that the grooves obtain. Furrows are unknown in the canals of the Batoidei; and it is in this order that the greatest degree of development is attained by the system. Dichotomization of the tubules appears in the higher, and becomes excessive in the highest, forms of either order. Types known to be sluggish in their habits are less abundantly supplied with tubules, and the system is not so complex as on the more active. It needs but a contrast of the Raiidæ and the Myliobatidæ to make this obvious. Forms which have changed their habits and become more addicted to resting on the bottom give evidence of the fact in the gradual deterioration and disruption of certain canals on the under portions of the body. That the canals are rather less subject to variation, that is, that they respond less quickly to its causes, than certain other organs, is intimated by the results of a comparison of the species of a single genus. Close genetic relationship is asserted by the canals of such species as *Dasybatus walga* and *D. nudus*, or by *Uraptera agassizii* and *Raia lævis*. Young specimens, or embryos, often serve better as guides to descent and affinity than old ones, since canals are present on the former which in some instances can hardly be found on the older ones. In the embryo the canal system takes on its generic

and specific peculiarities long before the characteristics of the outer skin are acquired, even before the shapes of body and fins, and the peculiar dentition, or the other features commonly relied upon to separate the forms and groups, have become available. Consequently, the various embryos may be recognized by means of the canals at periods when identification by the specific and generic characters ordinarily employed for the purpose of distinguishing them would be quite out of the question.

Dichotomized tubules do not appear to any great extent on the lower surfaces of such as habitually lie on the bottom. The tubules which occur on the ventral canals of such species most often have their external apertures at the border of the disk. On the Torpedinidæ it is altogether likely that disuse has led to the loss of the entire ventral portion of the system. Types addicted to flights through the water at a distance from the bottom have the tubules and their branchlets more alike on the upper and lower surfaces, as may be seen in such as the Zygobatidæ and the Dicerobatidæ. These and similar Rays have a greater aggregation of the tubules and branchlets toward the hinder portion of the disk, a distribution which suggests liability to danger from behind, possibly while the creatures are feeding. The modifications in position and outline which the cephalic canals have undergone on these families, through changes in shape of head, snout, and pectoral fins, and through change in the position of the mouth, become very prominent when directly contrasted with the same canals on such as the Trygonidæ or the Raiidæ.

The extent to which the canals may be used in classification is best illustrated by comparing the systems on the various species or groups. Necessarily the comparisons instituted below have been made very much as if the genera were composed of the species under examination. Further investigation of other species will, no doubt, bring to light differences in matter of detail, serviceable in specific diagnoses, and possibly such as may compel modification of our ideas of the generic characters; but the attempt has been made here to use only such features as are least liable to the minor variations. As the vessels have not yet been studied on one sixth of the whole number of species in the class, and as those on which the system has been worked out do not include representatives of all of the genera, it follows that a synopsis constructed on the material here gathered could only be a temporary affair. For this reason a short summary of differences is to be preferred to a synopsis giving only a few of the more prominent ones.

A connection of the cranials, instead of the laterals, by the aural, and the passage of the jugulars across the chest, at once separate the Holocephala from both the Galei and the Batoidei. The Batoidei are separated from the Galei by the possession of the pleural canals.

Chimæra, in the Holocephala, is marked by the grooves, instead of tubes, and Callorhynchus by the tubes, instead of grooves.

Among the Galei, on the base of the tail the lateral canals descend to the lower edge of the muscles in Chlamydoselachus, Heptabranchias, Heterodontus, Pristiophorus, Acanthias, and Somniosus, as in the Holocephala. Open corporal canals resembling those of Chimæra appear on Chlamydoselachus, *Heptabranchias maculatus*, and, in part, on Acanthias. On other genera the laterals maintain their position near the vertebræ of the tail, and the canals are tubular. On Scoliodon, Mustelus, and the Hammerheads the lateral makes a decided bend below the second dorsal fin; and it ends at or near the end of the vertebral column in Scoliodon, Triacis, Mustelus, Odontaspis, Scylliorhinus, Chlamydoselachus, Ginglymostoma, Cestracion, and Somniosus, not reaching so far back in others. Disregarding the course of the column in Isurus, it passes directly backward, ending at the edge of the muscles just above the lower lobe of the caudal fin.

The aural is behind the "ear openings," and more or less curved back in the majority of the Sharks; it is in front of the openings in Chlamydoselachus, bisected in Heptabranchias, curved forward in the middle in Acanthias and Chlamydoselachus, and nearly straight in Mustelus, Scylliorhinus, Heterodontus, and Somniosus. Sometimes, as in Pristiophorus, it is deeply curved backward, much as in the Holocephala, or in Dicerobatus.

The occipitals appear like continuations of the laterals, so slight is their change in direction, in Acanthias, Rhina, Heptabranchias, and Chlamydoselachus; others have the tubes directed more or less obliquely outward.

Somniosus is peculiar in that cranials, orbitals, and occipitals do not meet on the crown.

On the frontal region the cranial curves are shallow in Prionodon, Alopias, Isurus, Heterodontus, Acanthias, Somniosus, and Pristiophorus; decided in Scylliorhinus, Mustelus, Triacis, Ginglymostoma, and Rhina; more decided in Chlamydoselachus and Scoliodon; and excessive in Cestracion (Zygæna).

A majority have the orbital bent forward in its lower portion; in Cestracion, Heptabranchias, and Chlamydoselachus it bends backward.

In the suborbital, Scoliodon and Prionodon have a curve that reaches upward in front of the orbit. This curve goes farther forward than the eye in the greater number of the Sharks; it lies under the orbit in Isurus, Alopias, Cestracion, and Acanthias; it is absent in Heptabranchias, Somniosus, and Chlamydoselachus; and it goes forward of the nostril in Ginglymostoma.

Between the nostril and the median, in much the greater number of cases, the nasal canal is bent forward; this bend is either absent or faint in Isurus, Odontaspis, Alopias, Heptabranchias, Chlamydoselachus, Scylliorhinus, and Ginglymostoma. On Isurus the nasals meet the angulars; on others, as on certain Batoids, they meet the subrostrals.

A union of the nasals in front of the mouth on most of the sharks forms the median; no such union takes place on Acanthias, Heptabranchias, Chlamydoselachus, or Pristiophorus.

No connection between prenasals and rostrals appears in Heptabranchias and Somniosus.

Most often the jugular is directed toward the middle of the first branchial aperture; Alopias differs in having this tube pass below the gill opening.

The oral is continuous behind the mouth in Ginglymostoma; it does not meet the angular in Scoliodon, Prionodon, Triacis, Mustelus, Scylliorhinus, Acanthias, and Rhina; and it was not found in Heptabranchias, Somniosus, and Pristiophorus.

A general characteristic of the Batoids is seen in the pleural canals. At once on passing from the Pristiophoridæ of the Sharks to the Pristidæ of the Skates these tubes become prominent features.

The Pristidæ are affected by an excessive elongation of the rostrals and prenasals. Their pleurals are comparatively short, extending but little on the pectorals. The scapular branches are few, but one, a post-pleural, being present in the species sketched.

On the Rhinobatidæ post-pleural branches are more numerous. In general there is considerable resemblance between this family and the preceding. The anterior cephalic canals are shorter, and there is a sternal canal below the coraco-scapular arch.

All the Raiidæ are marked by greater extension of the upper pleurals on the pectorals. A strong branch extending back on the middle of these fins is apparently common. The prominent narrow fold in the subrostral varies in the different species: in Uraptera the fold has been so much narrowed as to bring its sides together. On the ventral surface of *Raia ocellata* the pleurals are obsolete.

The Torpedinidæ have lost the canals of the lower surface. Remnants of the missing vessels are found in the follicles of Savi, present on some. The pleurals and the orbitals unite directly, without the intervention of tubules. In Narcine the entire extent of the system is much less than in Torpedo, owing to the reduction in number and length of the tubules. Yet in these respects there is not a little variation in the species of Torpedo, as is seen by comparison of *T. californica* and *T. marmorata*.

In the Trygonidæ, as, further along, in the Myliobatidæ and their allies, we see a disposition to enlarge the system by means of curves, tubules, and dichotomous branchings much beyond what has been noticed in the Skates. Through the increase in length of the main tubes the courses of orbitals and suborbitals have come to be crossed by the pleurals on both upper and lower surfaces. The presence of a small enclosure, or more than one, on each shoulder, formed by scapular branches, pre-pleural or post-pleural, or both, is somewhat general in this section of the Batoids.

Potamotrygones as well as Thalassotrygones have the tubules of the pleurals on the lower surface massed anteriorly, comparatively few appearing under the posterior half of the disk. An obsolescent condition of the subrostrals obtains in Disceus and Potamotrygon; where parallel with the prenasals these tubes are merely lines of follicles, without apparent connection by their cavities, marking the paths of the canals. On the lower portion of the pleural of Potamotrygon there are rather few tubules; the sections of the oral are elongate and sinuous; the nasal meets the angular, and apparently there is a short sternal canal. On Disceus the tubules are very numerous on the lower pleurals, the parts of the oral are short and separated by some distance, the nasal and the subrostral meet, and there is an orbito-pleural plexus containing a large number of small areas. Differences similar in character, but less pronounced, exist on the upper surfaces of these genera.

Urolophus has no orbito-pleural plexus on the lower surface, its pleural tubules are not massed in front, and the suborbital is not provided with a long loop pointing forward as in Potamotrygon. It has a short sternal tube.

Tæniura resembles Urolophus more than it does the Potamotrygons. Like the former it has the pleural tubules distributed along the tube, and it has neither orbito-pleural plexus nor suborbital loop. It differs from Urolophus in the multitude of its branchlets on the upper aspect, in its pleural areas, and in the union of subrostral and nasal.

Dasybatus has a considerable part of the anterior portion of the lower pleural close to and parallel with the anterior edge of the pectoral. Along this section the tubules are numerous. Backward they are distributed sparingly, if present. The features possessed in common by the various species are best seen on the dorsal surface, since the tendency toward variation has been much more active beneath the disk. The suborbital alone is sufficiently different to distinguish the three species figured: in *D. nudus* it is excessively elongate, it encloses a peculiar series of spaces, and twice, in a couple of long reaches, it comes abruptly to an end; in *D. dipterurus* it is rather short and somewhat sinuous; and in *D. tuberculatus* it is greatly lengthened by a complex series of zigzag folds or convolutions.

Pteroplatea differs greatly from the other genera in the distribution of tubes and tubules on the dorsal surface. They are arranged to reach the margins around the entire pectoral, and, though numerous posteriorly, the branchlets are matted in multitudes in front. On *P. valenciennii* the tubules are most plentiful, on *P. marmorata* less abundant, and on *P. hirundo* still more scattered. These species differ in the branchings and areas on the scapular region, as also in the general arrangement and abundance.

The Myliobatidæ, through narrowing the pectorals at the side of the head, have had pleurals, orbitals, and rostrals brought close together under the orbit. Those types which have the fins most reduced, or absent, in this location, have these tubes arranged almost vertically one above another on the side of the face. This family and the Zygobatidæ agree in this respect; they also agree in restricting the dorsal canals to about half the distance from the vertebræ to the outer angle of the pectoral, in the arrangement of the lower pleurals in pairs of lines along the anterior margins or along the branchial and the abdominal areas, and in having a large portion of the oral longitudinally extended, as if folded with compression of the head, among the more noticeable peculiarities. We might also have included the Dicerobatidæ in the majority, if not in all, of these agreements. These families are readily separated by means of the cephalic canals. Forward from the fontanelle in the Myliobatidae the orbitals cross the rostrals, a position they do not attain in any of the lower families. *Myliobatis freminvillei* has longer canals on the rostrum and a less number of pleural tubules than *M. aquila*, and it has the subrostral separate from the prenasal. *M. aquila* has the shorter anterior cephalic tubes, the greater number of tubules on either surface, and has the subrostral joining the prenasal

near the median. Aëtobatus agrees with *M. aquila* in regard to junction of subrostral and prenasal; it differs from both of the sketched species of Myliobatis in such characters as would be more likely to be induced by greater compression of the head, as is seen in the foldings of the oral, deeper curvature of the aural, etc.

Zygobatidæ. — In this family the mouth, as compared with that of the Myliobatidæ, has been drawn backward closer to the gill openings or the coraco-scapular, and the snout, through reduction, and retraction to follow the mouth, has arrived at a position beneath the skull. The process of the change is well written in the foldings, sinuosities, and contortions of the cephalic tubes. Besides these particulars of characterization there are others, apparently resultant from a shortening of the longitudinal axis of the body, equally peculiar in this group. Of these are the scapular and posterior pleural foldings. The species figured differ in the number of cephalic tubules, in the scapular areas, in the post-pleural folds, and in the oral, which is divided in one species, united in the other.

Between the Dicerobatidæ and the Zygobatidæ there are more points of resemblance than between the former and the Myliobatidæ. There is more of a disposition to mass the pleural tubules posteriorly than in either; and the connection of the laterals across the vertebræ has not before been noticed in any of the Batoids. A further peculiarity occurs on the inner anterior section of the lower pleural, on which the tubules turn backward, as in *Myliobatis freminvillei*. The latter is no doubt only a specific character. Of the cephalic canals, it is hardly necessary to say anything, the distinctions arising from the peculiar shape of the head are so excessively marked. Yet, as is noted in the description of *D. olfersii*, the affinities existing between Dicerobatus and Rhinoptera are shown by the canals of both body and head.

The subjoined synoptic list furnishes a condensed illustration of the availability of the canal system in classification. Being based exclusively on the species here described and figured, some of them represented by single specimens, it is to be expected that study of new forms will necessitate modification and rearrangement.

CHONDRICHTHYOIDEA.

With the nasal canals in front of the nostrils;
  cranial meeting the aural
    HOLOCEPHALA.
    canals sulcate *Chimæra monstrosa.*
    canals tubular *Callorhynchus antarcticus.*
With the nasal behind the nostrils;
  cranial not meeting the aural
    SELACHIA.
    without pleural canals **Galei.**
    with pleural canals **Batoidei.**

Galei.

Oral not connected with angular;
  median longitudinal;
    cranial curves abrupt, deep
      Scoliodon terræ novæ.
    cranial curves shallow;
      an upward anal curve;
        jugular reaching toward upper edge of gill opening;
          anal curve prominent
            Mustelus canis.
        jugular reaching toward middle of gill opening;
          anal curve low
            Triacis semifasciatus.
        jugular curved downward
          Scylliorhinus caniculus.
      anal curve indistinct;
        nasals not meeting
          Acanthias americanus.
        suborbitals and subrostrals on top of snout *Rhina squatina.*
  median transverse;
    anal curve absent *Prionodon milbertii.*
Oral connected with angular;
  divided at the symphysis;
    cranials folded over themselves
      Cestracion tiburo.
    cranials not folded;
      suborbital and angular meeting;
        median transverse;
          jugular passing below gill opening *Alopias vulpes.*
        median longitudinal;
          jugular passing toward middle of gill opening
            Odontaspis americanus.
          jugular short, passing toward upper edge of gill opening
            Heterodontus philippii.
        spiraculars and gulars present
          Chlamydoselachus anguineus.
  not divided at the symphysis
    Ginglymostoma cirratum.
    suborbital and subrostral meeting
      Isurus punctatus.
Oral absent;
  aural divided;
    nasals not meeting
      Heptabranchias maculatus.
  aural entire;
    nasals not meeting
      Pristiophorus cirratus.
    nasals meeting *Somniosus carcharias.*

Batoidei.

Subpleurals in front of gill openings;
  pleural descending on edge of disk
    Pristis pectinatus.
  pleural passing through disk;
    sternal divided;
      rostrals and prenasals long
        Rhinobatus planiceps.
    sternal entire;
      rostrals and prenasals short
        Syrrhina brevirostris.
Subpleural and other ventral canals absent;
  tubules very short *Narcine brasiliensis*
  tubules medium;
    aural tubules very short
      Torpedo marmorata.
  tubules long;
    aural tubules long
      Torpedo californica.
Subpleurals at side of gill openings;
  tubules simple; a long post-scapular tubule;
    orbito-nasal at right angles with pleural *Uraptera agassizii.*

orbito-nasal parallel with pleural
Raja lævis.
subpleurals partly obsolete
Raja ocellata.
tubules with dichotomous branchlets;
pleural tubules distant from lateral and hinder margins;
subpleural tubules massed in front of head;
subpleurals and suborbitals forming a network;
subrostral and nasal meeting
Disceus strongylopterus.
no subpleural network;
no lateral tubules on subpleural;
subrostral and suborbital meeting
Potamotrygon motoro.
lateral tubules on subpleural;
subrostral and suborbital meeting
Urolophus halleri.
subpleural and suborbital meeting, very tortuous
Dasybatus tuberculatus.
subpleural and suborbital not tortuous;
orbitonasal a mere point
Dasybatus dipterurus.
no lateral tubules on subpleural; tubules massed in front;
suborbital forming a series of four incomplete areas
Dasybatus nudus.
pleural tubules reaching outer pectoral angles;
areas included by pleurals wider than long;
lower pleurals emerge two sevenths way from the median to tip of snout
Pteroplatea valenciennii.
lower pleurals emerge two fifths way from median to tip
Pteroplatea marmorata.
lower pleurals emerge half-way from the median to the tip
Pteroplatea hirundo.
pleural tubules reaching little, if any, more than half-way to the outer angle;
laterals not united across the vertebræ;
anterior cephalic tubes reaching forward from skull;
subrostral and prenasal united;
median transverse
Myliobatis aquila.
median vertical
Aëtobatus narinari.
subrostral and prenasal not united
Myliobatis freminvillei.
anterior cephalic tubes not reaching in advance of skull;
oral not crossing symphysis;
no long tubules on the occipital
Rhinoptera brasiliensis.
oral crossing symphysis;
long tubules on the occipital
Rhinoptera jussieui.
laterals united by tubes across the vertebræ *Dicerobatus olfersii.*

DESCRIPTIONS.

Chimæra.

Chimæra monstrosa (Plate II.) has open grooves throughout both corporal and cephalic portions of the canal system. The delicate membranes of the inner part of the furrows are protected by closely set scales which overhang from each edge. There are no tubules. On the snout the canals present a

peculiarly scalloped appearance, caused by the rising of short sections of the edges as prominent rounded flanges supported by ribbed cartilaginous expansions. At the end of each pair of these flanges the walls are lower, which gives an appearance of rounded holes into the grooves. Between the holes the edges are somewhat zigzag.

On the scapular region the lateral (*l*) makes a moderate curve upward; on the flank it is slightly sinuous; and on the anterior portion of the tail, near the forward end of the lower lobe of the caudal fin, it descends to the lower edge of the muscles, a position retained to the extremity. In its middle the aural (*au*) is bent back, forming an angle from which a short post-aural branch reaches toward the dorsal spine; the canal crosses behind the aqueducts. Aural and cranial (*cr*) are joined; they are connected with lateral and orbital (*orb*) by an occipital (*oc*) of moderate length passing downward and backward. The cranials converge to some extent on the forehead; on each side of the frontal holder they turn out a little, but approach again on the snout. Below the posterior border of the orbit the orbital meets the jugular (*j*) and the suborbital (*so*). From this point the suborbital passes forward to join the rostral (*r*) at the end of the snout, rising well up in front of the eye in an open loop, somewhat inclined forward. An individual variation appears in each of two specimens at hand: in one the angular (*ang*) unites with the jugular, in the other with the suborbital. At first the angular passes downward to the oral (*o*); thence it goes forward to the nasal (*n*) and the subrostral (*sr*). The jugular runs obliquely backward and continues across the throat in a broken line. Beneath the back part of the eye the oral leaves the angular, and may be traced across the chin in a series of dashes or dots. The nasal lies in front of the nostril; it bends forward and meets its fellow in advance of the nares, but forms neither median nor prenasals. From the suborbitals the subrostrals extend toward each other and unite in a median; a short distance posteriorly they diverge to meet the angulars. The second specimen differs from that just noted in having the angular united with the suborbital, and the jugular less noticeable on the throat. The first of these features is an approach to the condition in Callorhynchus, where angular, oral, and jugular connect with the suborbital, but not with each other.

Callorhynchus.

Callorhynchus antarcticus (Plates III., IV.) differs from Chimæra, and agrees with the majority of the Sharks, in possessing canals that are tubes, instead of furrows. On the flank the lateral rises a little in the scapular region; thence it is sinuous to the end of the dorsal; and thence stralght to a point above the lower lobe of the caudal fin, where it makes an abrupt downward bend to the lower edge of the muscles, which position it retains to the end.

In the middle the aural is much turned back; but it forms no angle and sends off no branch. Forward from the aural the cranials are gradually con-

vergent, more decidedly so in advance of the frontal holder (♂), and they approach each other closely on the thin portion of the proboscis. As in Chimæra, the occipitals connect the laterals and the orbitals with the aural and the cranials, instead of connecting the aural and the laterals with the orbitals and the cranials as in the Selachia. Orbitals and jugulars meet below the pupil of the eye. The suborbitals are very long; they pass quite to the end of the snout, and there meet the rostrals as the latter pass to the lower surface of the rostrum. A row of short pieces of canals across the throat serves to unite the jugulars. Under the fore part of the pupil the oral leaves the suborbital; it curves forward on the cheek and the chin, and backward behind the corners of the mouth. On the cheek it has what appears to be a more slender tube just in front of itself. Not far in front of the oral the angular descends toward the mouth from the suborbital. As it nears the lip it takes more of a forward course, and, following near the border of the rostral flap, finds its way down and backward to the edge of the lower surface, where it turns under and inward to cross the wing and meet the angular of the opposite side. After meeting the suborbital each rostral in its backward route approaches very close to its fellow, under the end of the rostrum, if it does not unite with it. Farther back they diverge, and each turns up a side of the snout, curving back as if to unite with the nasal. The union of subrostral and nasal has not been traced. In the adult specimens the oral and the jugular show tendencies to obsolescence.

Although there are great differences in the shape of the head in this genus and in Chimæra, in the arrangement of the canals in the two cases there is a great deal of similarity. One has only to suppose the snout of Callorhynchus shortened, so that the flap may be applied against the head, and the union of subrostral and nasal, if not already existing, to produce an arrangement essentially the same as that of Chimæra.

Scoliodon.

Scoliodon terræ novæ (Plate V.) represents one of the subdivisions of the genus Carcharias, as arranged by Müller and Henle. Comparison of this species with *Prionodon milberti*, a representative of another of these subdivisions, will give an approximate idea of the range of variation within that genus.

A small amount of curvature only is to be noticed in the thoracic portions of the laterals. Below the second dorsal they make a slight descent, then they rise rather higher than before, after which the canals retain the same relative height as regards the vertebral axis till they reach their terminations at its end.

In its middle the aural has a shallow backward bend; and it has one of similar depth in the opposite direction near each end. The occipitals are comparatively long; they are extended obliquely out toward the eye. A short distance from these canals, each cranial makes a short but decided outward

bend; in front of this, and between the orbits, it runs abruptly toward the middle of the crown, before reaching which it makes a broad deep curve, carrying the tube outward to a point opposite the hinder margin of the fontanelle, whence it passes in a nearly straight direction toward the tip of the snout. Before it reaches the latter, it descends to the lower surface. Soon after leaving the cranials, the orbitals sink deeply into the tissues of the side of the head; approaching the skin again, each makes a broad curve around the orbit, rising in front above the middle, after which it goes downward to meet the angular, nearly half-way from the eye to the nostril. The angular is rather elongate; its continuation, the jugular, ends in front of the middle of the first branchial aperture. The sections of the oral are disconnected and detached; the space separating them from the angular is about equal to that separating them from each other; their length is about two thirds of that of each mandible. At its forward extremity the short orbito-nasal meets the subrostral and the nasal; posteriorly it meets the suborbital and the angular. The nasals are nearly transverse, and would be quite so if not for a decided curve forward at the inner edge of each nostril. A short longitudinal median connects the nasals and the prenasals; the latter have a moderate degree of divergence, and unite with the rostrals.

Very prominent cranial curves, long occipitals, a shorter suborbital fold in front of the eye, and a more pronounced nasal curve, are among the most patent differences to be noted on this species as compared with *Prionodon milberti*. An approach toward the conditions existing on Cestracion is to be seen in the cranial, rostral, subrostral, and nasal curves, and in the great depth to which the orbitals have sunk in the tissues behind the eye at the side of the head.

Prionodon.

Along the trunk, the laterals of *Prionodon milberti* (Plate VI.) deviate but little from a right line. There is a small degree of curvature behind the occiput. Opposite the anal the downward bend is hardly perceptible. On the tail, above the anterior portion of the fin, the canal descends hardly half-way to the lower edge of the muscles; it keeps the same relative position as far back as to the hindermost of the vertebræ.

The aural is transverse, turned back a very little at each end. The occipitals reach toward the side, behind the eye; they are rather short. In the coronal region each cranial makes a long shallow curve inward. From the fontanelle they are nearly direct, converging somewhat; and they descend some distance behind the end of the snout. Depression of the head has brought orbitals and angulars close together, on the cheek. In front of the orbit, the suborbitals rise higher than the middle of the eye; the loop formed by them extends more than a diameter in front, and it is about half as far from the orbit to the junction with the angular. The subrostral is long, with a shallow curve around the nostril; the angular is long; the jugular is me-

dium; the orbito-nasal is short; the nasal is transverse, with a broad curve; the median is very short; and the prenasals are long and connected with the rostrals. There is a short disconnected oral behind each side of the mouth. In their principal features, the canals represented in this form are intermediate between those of Mustelus and Scoliodon.

Cestracion (Klein).

Forward, the laterals of *Cestracion tiburo* (Plate VII.) are nearly straight; backward, they have a pronounced curve, between anal and second dorsal, but do not descend much below the middle of the tail, and they stop near the end of the vertebral column.

The flatness of the head, the expansion of the snout, and the positions of nostrils and eyes at such great distances from the occiput, have caused some very peculiar contortions of the cephalic tubes. A small amount of backward convexity is presented by the aural. The occipital is elongate and turned toward the side. Between the eyes the cranial is very tortuous, turning upon itself several times before taking its way toward the rostrum, where it again makes a backward run before passing through. From the occipital the orbital goes outward and backward a short distance, then passes through, behind the lateral cartilages of the skull, to the ventral surface. Below the head the subrostrals tend laterally near the edges until about half-way from the snout to the eyes, where they ascend and run for a similar distance on the upper surface before descending again just in front of the eyes, thus passing around the nostril, and finally going with much directness to meet the nasal about half-way from the eye to the median. A great bend out in the direction of the eye is made by the suborbital on the way forward to its junction with the angular, the entire length of the tube being about three times the distance between the point of appearance on this surface and that of the meeting. The orbito-nasal is very short; it lies at right angles with the angular. Angular and jugular are about equal in length. Near the corner of the mouth the oral is bent toward the thorax; it is connected with the angular, but does not cross the symphysis. Were it not for a long narrow loop putting out toward the nostril the nasal would be described as nearly transverse. This loop has parallel sides, is slightly bent back, and has a tubule from its extremity. A median of moderate length gives rise to a pair of prenasals, which are somewhat curved, and which meet the subrostrals a little toward the side from the points at which the latter make their appearance.

An arrangement of canals such as that here described might be developed from a form like *Scoliodon terræ novæ* by crowding the snout back toward the skull and expanding the head at the sides. To push the long cranials back toward the occiput would bring about the identical curves appearing on the Hammerheads; in fact, the curves on Scoliodon are just what would naturally lead to such a result. Expanding the head would necessitate the appearance

of the subrostral on the upper surface to retain its position outside of the nostril, the latter being on the edge. And the orbitals, being behind the expansion, would sink deeper into the tissues; this also is simply going farther in the direction already partially traversed by the orbitals of Scoliodon.

Mustelus.

Anteriorly on *Mustelus canis* (Plate VIII.) there is hardly any departure from a right line in the lateral. Over the anal fin the canal rises; farther back, it descends to its former level, and, not going below the middle of the caudal muscles, it stops at the last of the vertebræ.

Comparatively little curvature is apparent in either aural or occipitals. The latter are short and diverge toward the cranials. In front the cranials converge; opposite the fontanelle they turn directly toward the side of the head for a short distance, then they run forward, almost straight, somewhat convergent, and pass through the snout before reaching the tip. At first the orbitals are transverse, but with a gradual curve they sweep below and about half its diameter in front of the eye, where they turn back and downward to meet the angular beneath the anterior third of the orbit. The angular is of medium length; the jugular is short, ending near midway from spiracle to gill opening. A short horizontal orbito-nasal connects with a long subrostral, in which there is but a slight bend at the side of the nostril. A prominent curve appears in each nasal, between the nostrils. The median is long and longitudinal. The prenasals are rather long; they connect with the rostrals. Behind each angle of the mouth there is a short detached oral.

The canal system of Mustelus closely resembles that of Triacis.

Triacis.

On *Triacis semifasciatum* (Plate IX.) there is hardly any curve in the scapular portions of the laterals. As in Mustelus, the anal curve is a broad one; the canal does not descend to the edge of the fin, and it stops at the end of the column.

There is a slight forward bend in the middle of the aural, otherwise it is almost straight. The occipitals are of medium length, and are divergent. In their coronal portions the cranials are nearly straight. At the sides of the fontanelle the bend is abrupt, but not deep. The rostral sections of these canals vary in outline, converge, and descend before reaching the end of the rostrum. Passing outward, the orbitals bend back slightly; they sink deeply into the tissues behind the eye, and extend in front of the orbit more than its diameter. A much more open loop is made by these tubes as they turn to join the angular than in Mustelus. The angular is of moderate length; the jugular is short and turned up toward the superior edge of the gill opening, as in Ginglymostoma, Scylliorhinus, and Mustelus. The orbito-nasals are short, convergent

forward. The subrostrals are moderate in length and slight in curvature. The nasals are transverse, broadly curved forward between the nasal valves. Approaching the symphysis, behind the corners of the mouth there is a pair of detached orals. A short median and moderate prenasals, the latter connected with the rostrals, complete a system closely resembling that of Mustelus and with remote likenesses to that of Scylliorhinus.

An embryo of two and a half inches agrees so well with the adult that it is readily identified by means of the canals. Without the aid of the system identification would hardly have been possible.

Isurus.

Isurus punctatus (Plates I., X.) by the fusiform shape of its body compels the laterals to diverge considerably along the middle of the flanks. With this exception they are tolerably straight, there being hardly any deflection above the anal, and but a scarcely noticeable upward turn on the tail. In reality the laterals cross the muscular portion of the tail, not following the course of the vertebræ, and they end at the lower (hinder) edge of the muscles close behind (above) the lower caudal lobe in front of the concavity in the posterior margin of the fin.

The aural is long, without prominent curves. The occipital is short, and nearly transverse. Both coronal and rostral curves of the cranials are long and shallow. The rostrals are short. In its downward course the orbital is waved a little; as a suborbital it joins the subrostral below the forward margin of the orbit. By its connections the short orbito-nasal would appear to be reversed in direction. In one specimen the angular bends downward behind the angle of the mouth to meet the oral, and the jugular makes an upward turn, then goes half-way to the gill, to bend up still farther at the end; in another case the angular and jugular form a single nearly straight line. The oral is connected with the angular, and runs but little beyond the corner of the mouth. At less than a quarter of the distance from the eye to the rostral tip, the subrostral appears on the lower surface; from this point it is longitudinal, faintly curving above the nostril. No nasal curve appears in the nasals. The short median is nearly transverse. About one third of the prenasal is bent abruptly to the side to meet the rostral.

Prominent among distinguishing characters are the caudal portions of the laterals, the reversed orbito-nasal, the transverse median, the curveless nasal, and the attached oral.

Odontaspis.

Odontaspis americanus (Plate XI.) exhibits neither scapular nor anal curves in the laterals. The canal remains near the middle of the tail, and stops a little forward of the last of the vertebræ.

The aural bends back in the middle a very little. The occipital is of mod-

erate length, and puts out directly toward the eye. On the crown the cranials are straight until opposite the fontanelle, where they make a shallow outward curve. The rostrals descend near the end of the rostrum. Starting down and backward, the orbitals make a broad curve around the eye until beneath it, where they become longitudinal and run more than a diameter forward from the orbit, before turning down and back, parallel with themselves, to join the angular. Both angular and jugular are long. From the angular the oral bends back around the mouth; it is not continuous across the symphysis. The long orbito-nasal bends down under the fore part of the eye before becoming longitudinal. Above the nostril the subrostral turns abruptly toward the nasal, in which there is no perceptible curve. The median is elongate and longitudinal. At the median the rather short prenasals bend outward, then turn forward to join the rostrals.

The type is characterized by absence of anal or caudal bends, by an elongate occipital, a slight curvature in the cranials, a longitudinal loop in the suborbitals, a prominent curve in the subrostrals, absence of a nasal curve, and by the junction of oral and angular.

Alopias.

Alopias vulpes (Plates XII., XIII.). A very great development of the canal system obtains in this Shark. There is no great difference in the main tubes from what may be seen in allied genera; it is in the enormous number, the length, and the amount of branching of the tubules, that unusual features are most patent.

Forward the lateral bends upward a little; at the base of the tail it follows the vertebral axis, keeping its position near the middle of the muscular portion, and ends a little in advance of the notch in the hinder extremity. Throughout the entire length the tubules are closely placed on the sides. Anteriorly, on the thorax, they are directed toward the back. Nearly all of those on the abdominal region are extended toward the belly. From the base of the ventrals to the end of the anal the tubules have numerous branches, some of which pass upward and others downward. On the tail the tubules are sent toward the lower edge of the fin.

The aural is long; in prominent curves it bends back in the middle and forward at each end. The occipitals are short. In the cranials the curves are shallow. At the crown the orbital starts back and down ; as a post-orbital it is vertical; and in the suborbital it sinks below the eye. Slightly in advance of the eye the suborbital turns back, and not far from the centre of the orbit, over the front edge of the mouth, is the union with the angular. The latter is of medium length. An uncommon arrangement of the jugular is seen here: the tube is long and passes below the gill apertures. The oral is elongate and connected with the angular; it makes a sharp bend around the corners, and is divided by a narrow interspace in the middle, behind the symphysis. At the

angular the orbito-nasals make an abrupt drop, beyond which they are longitudinal. The nasals are long, and have but a small amount of curvature. The median is short, and placed longitudinally. The prenasals are long, and abruptly bent to the sides to meet the rostrals. Opposite the nostrils there is a decided outward bend in the subrostrals.

A great number of long tubules exist on the laterals, and on some of the cephalic tubes. Those from the aural reach directly back. Those from the suborbital extend backward or downward; some of them connect with the angular or its tubules; all are more or less branched. Above the mouth the branches of the angular turn upward; behind the oral a few of them go downward, where, by meeting others from the oral, and by uniting among themselves, they form a network. On the upper side of the jugular the branches are much more numerous, but have not so many branchlets. Behind the angle of the mouth the tubules of the oral are longer and more branched.

There is a striking similarity in the canals of Alopias and those of Odontaspis. This may be seen in cranials, aurals, orbito-nasals, suborbitals, subrostrals, prenasals, nasals, angulars, and orals; and it appears fully to warrant placing these genera side by side in a systematic arrangement of the Galei.

Heptabranchias.

Heptabranchias maculatus (Plate XIV.). On the flanks of this species the canals are shallow furrows, protected by enlarged overhanging scales of the shagreen on the edges. In front the grooves commence above the forward portions of the bases of the pectorals; all the canals farther in front are tubes. Another specimen shows alternation in the lateral, between the aural and the continuous lateral furrow, of irregular lengths of tube and groove. Over the anterior lower lobe of the caudal the furrow bends downward in the direction of the fibrous portion, which it approaches more gradually backward, and it ends at the notch between the lower and the hinder sections of the fin.

The aural is divided by an interspace, behind the openings of the aqueducts, as in *H. pectorosus*. A small amount of outward curvature marks the elongate occipitals. At each side of the fontanelle the cranials bend out in a broad curve toward the side of the head. In front of the nostrils the rostrals turn back toward the subrostrals, but apparently without meeting them. These tubes seem to be separated, just above the nostril, by a short interspace. On the top of the head, again, the orbital is directed outward and a little forward; on the side it goes down and backward, without forming a suborbital, to join the angular and orbito-nasal. The latter is very long, and takes the place of the suborbital. Jugular, angular, and orbito-nasal form a single longitudinal line; the first is short, ending in front of the middle of the first gill cleft, the second is of moderate length, and the third is as long as both of the others. The nasal is of moderate length, curves strongly toward the median line, but does not meet its fellow, from the other side, to form a median. The pre-

nasals bend out toward the rostral, without approaching closely, then pass forward and end blindly near the tip, at a considerable distance apart. Above the front edge of the mouth the subrostral meets the nasal in a sharp angle. The nasal curve is comparatively slight. Traces of an oral were not detected.

Excessive thinness of the skin, by bringing the canals so close to the surface, favors the presence of furrows rather than tubes, or, to go still further, leads to the disappearance of the canals altogether, as in case of the orals of this and other species.

Characteristic features of the system on this shark are the isolation of the prenasal, the length of the orbito-nasal, the suppression of the suborbital, the direction of the orbital, the bisection of the rostral, the division of the aural, and the open lateral tubes. Several points, in occipitals, cranials, orbitals, and orbito-nasals, recall similar ones in Chlamydoselachus; the latter, however, is widely withdrawn by consideration of its lack of division in aural and rostrals, the position of its prenasal, and its possession of oral, gular, and spiracular canals.

H. pectorosus is, in most particulars, similar to *H. maculatus*. Its laterals end about two fifths of the length of the tail in advance of the extremity, making a decided and broad curve downward to the fibrous part of the caudal.

A specimen of *H. cinereus* has closed corporal canals, or tubes, of similar position and outline as the two species of this genus already noticed, but reaching a little farther toward the caudal notch than in *H. pectorosus*.

Chlamydoselachus.

Chlamydoselachus anguineus (Plate XV.) has the laterals open throughout their whole extent, with the exception of less than an inch immediately behind the aural. From each edge enlarged scales overhang the groove, enclosing it in a measure and protecting it. Along the flanks the canals are nearly straight. The caudal curve is very gradual in one specimen, more abrupt in another, and on one side of the second descends, then rises to repeat the curve. On the body, the canal lies a little above the crease between the muscles of the back and those of the flank. On the tail, its track lies a little below the middle of the muscular portion; it continues thus, with a few slight breaks posteriorly, to within an inch of the end of the vertebral column, where it stops.

In the sketch the courses of the closed cephalic tubes are indicated by lines of dots, each of the larger of which marks the opening of one of the short tubules. The aural is closed. It has no tubules. Contrary to what obtains in other Galei, it lies in front of the so-called ear openings. These openings, however, are at the ends of tubes the inner extremities of which are in front of the canal. The canal is nearly straight, bending slightly forward in the middle and a little backward near each end. The occipitals are long and

extend forward with a very slight trend outward. On the crown the cranials are parallel. At the sides of the fontanelle they bend abruptly outward, and, as rostrals, run near the edge of the snout for some distance before going to the lower surface. From the cranials the orbitals run outward and somewhat forward; near the side they turn backward and downward toward the corner of the mouth. They end some distance behind the eyes. A long angular joins the short jugular and the very long oral, which reaches almost to the symphysis. At the end of the jugular near the middle of the first branchial aperture, there are two branches not found in any other of the Sharks examined: a *spiracular* (*sp*), turning upward and forward toward the spiracle, and a *gular* (*g*), turning down and forward near the median line, and finally uniting with the oral a short distance from the inner end. Below the eye, in the position usually occupied by the suborbital, lies a very long orbito-nasal. The nasal is of moderate length, and curves broadly in its posterior half. The subrostral is a little shorter than the nasal; it bends upward over the nostril. Apparently the prenasal is reversed in direction, meeting the nasal in front and running backward to join the subrostral. Like the corporals, oral, gular, and spiracular are open grooves. In the spiraculars and gulars of this Shark are found the nearest approaches to the pleurals of the Batoidei.

Distinguishing peculiarities of the system on this type are seen in the possession of spiracular and gular canals, in the position of the prenasals, and in that of the aural, with regard to the ear openings. Similarity in the orbito-nasals occurs in Heptabranchias. Somniosus by the same canals is intermediate between these genera and others of the order.

Ginglymostoma.

Ginglymostoma cirratum (Plate XVI.). Over the shoulders the laterals have little outward curvature; in the anterior part of the tail they drop somewhat abruptly from the middle to the lower portion of the muscular band, near the edge of the fin, where they continue, ending with the vertebral column.

This form has a short broad head, and a very short snout. If compared with one of the long-snouted species, it will be seen that there is a tendency toward the transverse in the cephalic canals, which in those forms are nearly or quite longitudinal. The aural is long, bending backward a little in the middle, and as much forward toward each end. The occipital is of medium length; it runs obliquely outward, with a slight curve toward the spiracle in the middle. From the end of this canal the cranial turns rather sharply toward the crown; it then passes forward, diverging a little from its fellow until opposite the fontanelle, where it turns outward with less curvature than in Scylliorhinus. Approaching the edge, the rostrals run parallel with it until near the tip, where they descend. The orbital is rather short. The suborbital is much longer and passes forward more than three times the diameter of the orbit; above the nostril it turns back, forming an angle, and meets the subrostral a short distance forward from the eye. Angular and jugular are short; they are directed up-

ward some, toward the top of the first branchial aperture. Behind the corner of the mouth the oral makes a strong backward curve; the tube is a long one; it crosses the symphysis and meets with the angular. Posteriorly the orbito-nasal curves upward to meet the angular; the tube is elongate and nearly horizontal. The nasal is long, sinuous, and almost transverse. Contrary to what might be expected on a short snout, the median is long. As if reduction in the length of the snout had proceeded faster than in that of the tubes, the prenasals appear as if pushed back and folded on themselves; each is turned abruptly toward the side, and bent into two folds. They unite with the rostrals.

Prominent distinguishing features in this shark are the caudal canals, scapular curves, complete oral, long suborbitals and orbito-nasals, and the folded prenasals. Of the genera studied it approaches Scylliorhinus most closely.

Scylliorhinus.

Scylliorhinus caniculus (Plate XVII.) has scarcely any curvature in the laterals, and they end with the column, not going down to the fibrous portion of the caudal fin.

A slight sinuosity affects the aural. The very short occipital is directed toward the eye. Behind the fontanelle the cranials approach the median line in a broad curve: in front of this, they turn abruptly out toward the edges of the snout. Just before it joins the prenasal, there are several curves in the rostral: in descending it runs forward, downward, inward, backward, and outward. At the side of the nostril there is a prominent curve in the subrostral. The suborbitals are longitudinal below the orbit; at its forward edge they pass down and backward to meet the short orbito-nasals. The nasals are almost straight and transverse; the median is short; and the prenasals, sinuous and moderately long, unite with the rostrals. From the angular the jugular curves up toward the upper edges of the gill opening, which it does not reach. Behind each angle of the mouth there is a short disconnected oral.

Heterodontus.

On *Heterodontus philippi* (Plate XVIII.) the laterals diverge a little, behind the occiput; farther back they are straight, without a curve over the anal fin, until they reach the tail, above the lower lobe of which they descend to the lower edge of the muscles. As it nears the end of the column, the canal becomes a furrow.

Lateral and aural form a continuous curve, and are connected with the cranial and orbital, which form a similar curve, by a very short occipital. The cranial bends are broad, but not at all deep. This is true also of the suborbital, which reaches nearly a diameter in front of the orbit, then drops vertically on the subrostral. Angular and jugular are both very short. The oral joins the

angular, but does not cross the symphysis. The orbito-nasal is long. In passing the nostril, the short subrostral makes a decided curve. Behind the nostril the nasal is bent toward the mouth. The median is very short. From the median the short prenasal goes directly to the side, joining the rostral.

By the canals either Odontaspis or Ginglymostoma shows more affinities with Heterodontus than does Acanthias. The differences in dentition between the latter genera are scarcely greater than those apparent in the canal systems.

Acanthias.

Acanthias americanus (Plate XIX.). Backward from the shallow scapular curve, the laterals of this species are nearly straight. Above the widest part of the lower lobe of the tail, the tube makes a slight bend upward; it does not follow the vertebral column, but gradually approaches the lower edge of the muscles, and stops in front of the last vertebra.

In the middle, towards the ear openings, the aural is bent forward. A continuous longitudinal line is formed by the elongate occipital and the lateral. At the orbitals, the cranials make a rather sharp curve; opposite the fontanelle, they make a broad and shallow bend. The upper portion of the orbital is sinuous; behind the eye it is thrown backward; and beneath the orbit it goes but half-way before turning back in a sharp angle to join the angular. Jugular and angular together are short. The orbito-nasal is long, and is bent downward from the suborbital. By the side of the nostril there is a decided bend in the subrostral. The nasals are long and bent so that the curves in each approach the outlines of a Z; they do not meet to form a median, but run close together as in Pristiophorus. Near the end of the snout the prenasals converge, without seeming to join; they are located some distance from the rostrals. The tubes are of large calibre, and the tubules are numerous and short. A short oral lies close to each angle of the mouth, entirely disconnected. On the tail, for a short distance from the end, the canal is open. Figure 6 shows the arrangement of the scales and the form of the portion of the canal included between the dotted lines.

An embryo of two and a quarter inches has tubes similar to those of the adult, but the tubules are shorter or absent.

Somniosus.

Somniosus carcharias (Plate XX.) has tolerably straight tubular laterals. They extend on the middle of the muscular portion of the tail, running as far back as the hinder edge of the anterior lower lobe of the caudal fin; thence they descend to the lower edge of the muscles, above the fibrous portion, where they continue to the end of the column.

Among the cephalic canals a very peculiar arrangement occurs on the occiput: the aural is transverse, and has its ordinary position; from its ends the occipitals curve forward and inward, and end anteriorly without connecting with

other tubes; a short distance in front of their ends are those of the orbitals, also disconnected; and still farther in front are the posterior extremities of the cranials, like the others, making no connections. The orbitals pass directly outward, then downward and forward, meeting the angular below the hinder portion of the eye. At the start the cranials are transverse, they soon bend forward, and, making very open curves around the fontanelle, becoming rostrals, converge toward the end of the snout, before reaching which they pass through to the lower aspect. As subrostrals they go back and outward, making a loop on the side and top around the nasal chamber, and pushing farther back to meet the nasals. In comparison with that of other genera, the orbito-nasal is rather long; it extends below the greater portion of the orbit. A prominent curve toward the nostril marks the middle of each of the elongate transverse nasals. From a median of more than ordinary length the prenasals diverge and run forward, ending abruptly, under the tip of the snout, without joining the rostrals. The angulars are of moderate length. The jugular is short. An oral could not be found. The tubules are numerous, short, and provided with large apertures.

Especially noticeable among the peculiar features met with in this species are the separation of the orbitals and the cranials from the occipitals, the isolation of the prenasals, the supranarial curve of the subrostrals, the length of the orbito-nasal, the lack of the oral, and the caudal curve of the lateral. The coronal arrangement of the cephalic canals, and the subrostral curve, distinguish the genus from any of the other genera noted here. The orbito-nasal and the disposition of the lateral on the tail are intermediate between sharks like Heptabranchias and the majority of those of higher rank. In Cestracion (Zygæna) only of the other Galei have we seen the subrostral return to the top of the snout.

Rhina.

Rhina squatina (Plate XXI.). With the great depression of the body of this Shark, the lateral has to some extent been carried outward on the thoracic and the scapular regions. Excepting slight waves in the outline, there is hardly a deviation from a straight line in the tubes on the sides of the tail. The canal does not reach quite to the hindmost vertebra. Above the thoracic region near the aural a few of the tubules reach toward the median line. Elsewhere along the whole length of the laterals the tubules are short and directed out.

In consequence of the anterior position of the mouth and the shortness of the snout, the canals of the front part of the head are greatly reduced in length. Subrostrals, prenasals, and other tubes that in the balance of the Sharks are confined to the lower surface, have been brought to the top by depression of the head. The aural is long, curves backward slightly, and has a few tubules extending toward the shoulders. The occipitals are long, and divergent forward. On the frontal region, the cranials curve toward each other;

their tubules, as those of the occipitals, start out, but turn and cross the tubes toward the middle. Opposite the fontanelle the cranials make a broad open bend, from which the short rostrals pass about half-way to the middle of the mouth. From the front end of the rostrals the subrostrals turn back, around and behind the nostril, to meet the nasals on the sides of the face. The prenasals lie on the upper surface; they are nearly transverse, and turn back at the ends as if to join the rostrals, but without making a junction. Apparently the very short median is vertical. The orbitals are entirely on the upper surface. From the cranials, they go obliquely outward until past the orbit, then, turning forward at a right angle, the suborbitals run a short distance beyond the eye, where they turn out and backward, making a deep loop, convex in front. They meet the angular opposite the eye. Both angular and jugular are on the top of the disk. The orbito-nasal is on the side of the face; it is comparatively elongate, running from opposite the middle of the orbit to within a short distance of the nostril. The orals and the nasals belong to the lower view. The former are elongate, disconnected, and do not reach the symphysis; the latter are moderate and transverse, with a shallow curve forward toward the middle. The tubules from the suborbitals are rather long and pass outward; they, like the others, are unbranched.

The appearance of all the tubes, except orals and nasals, on the top, looks as if resultant from depression that had caused great expansion of the ventral portions of the body, and but little of the dorsal. This peculiarity alone would serve to distinguish the genus from the other genera. There is nothing in the canal system that favors the idea of close affinity with the Batoidei.

Pristiophorus.

Considerable uncertainty exists in connection with several points on the sketch of *Pristiophorus cirratus* (Plate XXII.), because of the bad condition of the specimen, a dried skin.

Back of the head the laterals turn outward somewhat; on the tail they appear to lie near the middle of the muscular portion, stopping at the end of the column.

The halves of the aural meet in a sharp angle at the middle; behind the openings of the aqueducts they form a V, from the apex of which a short tube extends directly back. A low inward sweep is made by the cranials, on the crown. Beneath the eye the orbital does not quite reach the front edge of the orbit; turning backward, it descends to join the angular on a vertical from the centre of the pupil. The angular is longer than the jugular. Apparently there is no oral. The orbito-nasal is rather long; and, with the angular and the subrostral, it forms a longitudinal line. In front of the mouth the nasal is turned back; it has a moderate nasal curve, and does not connect with its fellow to form a median. Prenasals and subrostrals are very long. In the specimen they cannot be followed near the end of the rostrum.

There are marked resemblances between this Shark and Acanthias, which

are at least suggestive of closer affinities in the distant past. These are brought prominently forward in comparisons of such tubes as the medians and suborbitals of the two forms.

Pristis.

Posteriorly the laterals of *Pristis pectinatus* (Plate XXIII.) are straight. On the tail there is a slight downward tendency, and the canals end near its extremity, at the lower edge of the muscles. Anteriorly, above the thoracic region, they are drawn toward each other; at the shoulder each makes an outward bend, from which the scapular and the post-scapular branches extend. A comparatively small area is enclosed by the pleural; from the shoulder the tube runs out and backward, then it turns forward, along the inner edge of the pectoral fin, to meet some of the tubules from the orbital, near the hinder part of the orbit, after which it makes a sharp bend and goes back a short distance parallel with its former course before passing down the side to the lower aspect, about opposite the aural. One or two post-scapular branches, together with the posterior pleural tubules, form a network of branchlets on the pectoral. Lateral, pleural, and suborbital possess slender tubules. Similar ones on the rostral have delicate branchlets.

On the ventral surface the pleurals run toward the gill openings, in front of which, about one third of the distance to the mouth, they meet the jugulars. The space included by these tubes is small.

The aural is deeply bent backward. A short occipital connects it with the orbital. The latter goes close below the eye and in front of it, about half a diameter, passes to the lower surface around the edge. Near the fontanelle the cranials diverge slightly, making a shallow bend; near the end of the rostrum they converge, but diverge again at the tip; in general, their course is tolerably direct. These, as the other tubes of this surface, are beset with a great many very fine short tubules.

Angular and jugular are moderate. The orbito-nasal is short; in front it meets the suborbital and the subrostral. Only a small portion of the suborbital is to be seen from below. The subrostral is much elongated, has a waved course, and is bent prominently forward in front of the nostril. The nasal is transverse, and waved in outline. The median is longitudinal and short. From it the prenasals turn abruptly outward, toward the nostrils, before taking a course of tolerable directness toward the rostral extremity. Close to the latter they appear as if crowded back, so as to make a fold directed toward the median line. Behind each side of the mouth there is a disconnected oral; toward the middle the tube bends forward, at the outer end it is turned back in a hook.

Although there is much resemblance between the majority of the canals of *Pristis* and those of *Pristiophorus*, the presence of the pleural and the scapular branches fixes the position of the former in the Batoidei.

Rhinobatus.

Rhinobatus planiceps (Plate XXIV.). From the shoulder girdle to their ends on the tail the laterals of this species are nearly straight. At the pectoral arch the scapular curves carry them outward, and back of the head they approach each other. Posteriorly they send numerous tubules outward; anteriorly others are sent inward and backward. Behind the scapular there are four post-scapulars, each of which has two or more tubules near the end. There is more lateral curvature in the pleurals in this genus than was seen in Pristis; there is also a more intimate connection between them and the suborbitals, by means of four or more of the tubules. Opposite the forward part of the orbit, about half-way between it and the margin, the pleurals pass through the disk, after sending numerous tubules on the pectoral. These pleural tubules are of two kinds, one stronger, longer, and straighter; another finer, shorter, and crookeder, distributed among the first. The course of the pleurals on the lower surface is short; they meet the jugulars in front of the first branchial aperture.

The aural curves back in the middle. A slight divergence obtains in the short occipitals. In front of the eye the cranials curve outward sharply; they approach each other nearest along the middle of the rostral cartilage. At the end of the suborbital a branch is sent backward; in front of the eye its tubules extend both inward and outward; and still farther in front they are sent toward the margin. Instead of going around its edge, the suborbital passes through the disk very near the border. On reaching the lower surface this tube makes a broad curve back, and joins the subrostral opposite the nostril. A short orbito-nasal connects it with angular and jugular, both of which are short. The nasal is bent back behind the nasal valves. The median is very short. Near the middle of their length the elongate prenasals are curved toward each other. The oral crosses the median line behind the mouth, but is disconnected from the angular. Around the anterior border of the abdominal chamber, beneath the coraco-scapular arch, there is a sternal canal, which differs from the others in being more open; it does not cross the middle. This canal was not seen in Pristis.

Syrrhina.

Syrrhina brevirostris (Plate XXV.). A description of the canal system in this species would duplicate that of the preceding, excepting that rostrals, subrostrals, and prenasals would be found to be greatly shortened. Other points of difference, less important, are seen in the smaller number of branches of the tubules and the undivided condition of the sternal. A study of the canals of this species discloses little that favors separation from *Rhinobatus*, since it differs less from species of that genus than some of them do from each other.

Uraptera.

On *Uraptera agassizii* (Plate XXVI.) the upper surface is pretty well covered with tubes and tubules. On the ventral aspect the main tubes are all present, but the tubules are few and short. There is nothing in the canals that will distinguish this genus from *Raia*.

On the shoulders, the laterals are thrown decidedly outward; farther forward, they make a broad curve toward the vertebræ; and they converge toward the base of the tail. Their tubules are of medium length and are most numerous above the abdominal region. The pleurals reach far out on the pectorals, enclosing an area, convex forward, somewhat lenticular in shape. At the angle opposite the shoulder they send back a strong branch with many tubules on its outer side. The most of the pleural tubules pass forward; a few, especially of those near the anterior border, turn back. Opposite the eye the pleural is connected with the suborbital by several tubules; thence it bends toward the margin and descends about half-way from the orbit. A strong postscapular goes to the hinder angle of the pectoral; the greater number of its tubules are directed outward.

The occipitals are short and greatly divergent. Between the eyes the cranials curve toward each other; in front of the orbits they bend apart; and on the rostrum they converge gradually to their points of descent, near the end. Outward from the curve in front of the orbit a tuft of tubules extends from each. The suborbitals take a tolerably direct course to the end of the snout, but pass down some distance before reaching it.

On the lower surface, the pleurals bend out opposite the first gill cleft and inward opposite the shoulder girdle, in both the backward and the return courses. They neither reach back behind the middle of the abdomen, nor out to the middle of the pectorals.

The orbito-nasals are elongate, converging in front. The lower suborbitals are only of moderate length, diverging backward. On the greater part of the length of the snout the subrostrals are parallel with the prenasals; leaving the latter finally, they pass outward and then forward to make a close fold on themselves before taking a transverse direction in which they meet the suborbitals. At the inner edge of the nostril the nasals make a sharp bend, then, converging forward, they unite to form a short longitudinal median. From the median the prenasals at first bend outward rapidly, then converge gradually toward the tip, near which they end without connections.

The following peculiarities are among the more likely to prove characteristic: the shape of the pleural area, the short occipital, the length of the tubules, the closeness of the fold in the subrostrals, and the longitudinal median.

Raia.

Raia lævis (Plates XXVII.–XXIX.). Some resemblance is seen in the shape of this species and that of Uraptera, and there is still more in the arrangement

of the main canals. If these vessels alone were taken into consideration, more than specific distinction would not be accorded the two types.

In comparison with the preceding the laterals on the smooth Skate approach each other more gradually behind the shoulders and more abruptly in front of them. Over the gills the branchial area is wider, and in general it is more irregular in outline. The majority of the tubules on the hinder branch of the pleurals run forward or outward, and on the post-scapular, toward the hinder margin, a number of them turn backward.

The occipital is rather long. At the side of the eye a branch, from the suborbital, turns back in the direction of the branchial area. Three or four tubules connect the orbitals with the pleurals; the latter go down near the margin, more than half the length of the snout in front of the skull.

Beneath the disk the subrostral is parallel with the prenasal more than half the distance to the mouth; it then turns outward, and returning makes a sharp curve and fold, not quite as close and complete as that of Uraptera, after which it goes back obliquely, instead of transversely as in that genus, thus bringing about a shortening of the orbito-nasal. The pleural lies close by the side of the angular and orbito-nasal; opposite the mouth it bends outward a short distance, then stretches back almost directly toward the posterior angle of the pectoral; and about as far back as the middle of the abdomen it turns to the coraco-scapular arch to meet the jugular. The space included is narrow in front, and much broadened at the shoulder girdle. There is a moderate amount of curvature in the nasal. The median is transverse. At the median the prenasals make a broad bend; they are not connected in front. The oral is disconnected, and is in two sections.

Plate XXVII. shows the tubes and tubules of the upper surface; Plate XXVIII. gives (fig. 1) the hyaline mucous ducts of the "ampullæ of Lorenzini," and (fig. 2) the main tubes of the canal system of the same surface; and Plate XXIX. contains a view of the lower side of the head in fig. 1, and a sketch of the upper surface in fig. 2.

Raia ocellata (Plate XXX.) is one of the species with shorter snouts. In consequence of the rostral shortening, the lengths of the prenasals and of the rostrals have been decreased so much as to bring their forward extremities almost back to a transverse line from the end of one suborbital to that of the other.

Above the thoracic region the curves of the laterals are shallower, and the scapular bends are less prominent, than in *R. lævis*. The pleural areas are subtriangular, broader posteriorly. The posterior branch of the pleural is the longer. A strong post-scapular extends from the shoulder obliquely out to the posterior margin. This tube is provided with tubules on its outer half. Laterals, pleurals, and orbitals also have tubules, which are more or less irregular in regard to length.

The occipitals are of moderate length. The cranials have a prominent curve opposite the fontanelle, and another near the orbitals; their tubules are short, with the exception of several in front of the orbit.

On the ventral surface the pleurals are entirely absent, from the posterior jugular extension. A moderate length obtains in the orbito-nasal. The curve in the subrostral is very prominent, and a trifle more open than that of *R. lævis*. A decided curve appears in the nasal. It is difficult to determine whether the median is longitudinal or transverse, it is so very short. Near the mouth, the prenasals separate widely; forward, they are convergent but not connected. An oral appears behind each half of the lower jaw.

Torpedo.

Torpedo californica (Plate XXXI.) goes much beyond the following species in respect to the amount of surface covered by the tubes and tubules. On the shoulders, the curve, or, better, the scapular angle of the laterals, extends farther out, and, the batteries occupying a larger portion of the disk, the pleurals are carried nearer to the margins. As in that species, pleurals and suborbitals seem to form a continuous tube.

The aural is longer and straighter and in front of it the cranials converge more. The rostrals extend farther toward the border, and are better provided with tubules than in *T. marmorata*.

At the sides of the suborbitals, and the thoracic portions of the laterals, long tubules pass out upon the batteries, nearly across them. A marked contrast is presented by this distribution when compared with that of the following, or of Narcine, in both of which the tubules venture little if any over the surface of the batteries. A number of long tubules put out from the aural toward the shoulders. Behind the angles on the pectorals formed by the pleurals, there is a strong tubule with several branches; elsewhere the tubules are simple.

There is much irregularity in the cephalic tubes, and it is probable that there is considerable variation between individuals of the species in regard to suborbitals and rostrals. In fact, there is great variance in the tubes of opposite sides of the head of a single specimen. This is well illustrated by dissections of the head of *T. occidentalis*.

Torpedo marmorata (Plate XXXII.) accords substantially in the arrangement of the canals with *Narcine brasiliensis*, but the tubes are longer and more crooked, and the tubules are of much greater length. On the back over the branchial region the laterals are considerably curved. Surrounding the large batteries the pleurals approach very near to the front margins of the disk. These tubes unite directly with the suborbitals. The occipitals are long. The cranials make a rather sharp curve in front of the eye, and they disappear before reaching the end of the rostrum. Among the longest tubules are those situated posteriorly on the pleurals and the orbitals, and anteriorly on the laterals.

This genus agrees with *Narcine* in the absence of the canals on the lower surface.

Absence of post-scapulars, or, better, the backward position of the pleurals

where joined to the laterals, is an approach toward the Trigonidæ rather than toward the Raiæ.

The lack of canals on the lower surface and the junction of pleurals and orbitals sufficiently distinguish the Torpedoes from other families.

Narcine.

Narcine brasiliensis (Plate XXXIII.). Apparently there are no traces of the canals on the ventral surface. On the back there is a very simple arrangement of the system. The lateral passes directly to the end of the vertebral column. Only a moderate degree of prominence is given the scapular curve. Rather widely separated at the shoulders, the laterals converge toward the back of the head. The tubules are short and not many. At the outer edges of the batteries the pleurals encroach but little on the pectorals. Half-way from the eye to the margin they unite directly with the suborbitals.

The occipitals are long. About midway from the eye to the end of the snout the cranials dwindle and disappear, after sending off a group of short tubules in front of the eye. The curve around the eye described by the orbital is somewhat regular, and the canal ends near the margin. It sends out a couple of short branches near the spiracle, and some shorter ones in front of the junction with the pleural. A strong tubule reaches backward from an angle in the pleural, opposite the scapular bends. From the lack of branchlets, the small size of the tubules, etc., the total length of the system is much below the average of the order.

Potamotrygon.

Potamotrygon motoro (Plate XXXIV.). Upon the shoulders of this species the laterals bend outward in a variety of curves. The anterior of these, the greater ones, are concave, the posterior convex. A very little behind the girdle the pleurals are met. There are two pre-scapular tubules, which do not enclose an area. Behind the pleural there are several post-scapulars more or less disposed to unite soon after leaving the main tube. The pleural starts from several branches which form scapular enclosures. Backward from the aural the laterals describe the outlines of a goblet, with the bowl extended forward, and closed by the aural. The occipital tubules are not far behind the ends of the latter. At the fontanelle the cranial curves are but moderate. Tubules are numerous on the head, and backward; in general they branch two or more times. From the laterals the pleurals pass backward and outward, rather more than in the sketch, until well out on the fin, where they form a somewhat sharp angle and turn forward in a broad curve; in front of the eye they turn inward, and, passing under the orbital, they descend at the fore part of the skull. Long tubules, with small groups of branchlets at their ends, extend laterally toward the margins. Two or more tubules join the pleural and the orbital. A branch goes back from the orbital at the eye, and, in front of the

orbit, five or six long tubules reach toward the anterior border. The orbital goes down at the side of the rostral, not half-way from the skull to the end of the snout. Nearly or quite all of the tubules on this surface are branched.

On the lower aspect the pleurals pass toward the front margin, and, running parallel with it, send out a number of simple tubules; afterward, along the middle of the fin, they take a course of some directness to the posterior extension of the jugular, a little distance forward from the pelvis. A single tubule marks the turning point. Bending around and back, as far as the mouth, in a waved course, the suborbitals make a long loop forward. Behind this loop they extend toward the gill apertures; in front of the latter they turn toward the nostrils and meet the subrostrals opposite the mouth. The orbito-nasals are of medium length, the nasals are long and moderately curved, the median is short, and the prenasals are elongate and close together. Between the nostrils each subrostral makes a deep bend, on the nasal valve; they end, at the side of the prenasals, in a series of rings or capsules connected with each other by thin transparent tissue, which only near the mouth presents the semblance of a tube. These rings are closed follicles, which do not appear to be connected with the surface; they seem in most respects identical with the follicles of Savi, and trace their origin to obsolescent canals, of which portions surrounding certain nerve endings have persisted and become closed sacs. Rings and enlargements also are seen in the front portions of the prenasals. On each side of the symphysis, near the teeth, a crooked oral reaches about half-way to the first gill cleft. A short sternal crosses the middle in front of the pelvic spine.

Distinguishing peculiarities appear in the presence of both pre- and post-scapulars, in the isolation of the subrostrals, in the groups of tubules on the front sections of the ventro-pleurals, and in the oddly shaped loop in the suborbitals.

Disceus.

Disceus strongylopterus (Plate XXXV.). One of the most peculiar canal arrangements to be found in the order occurs in this genus. Pre- and post-scapulars are both present, and, outside of the prominent scapular curve in the laterals, there is a pre-scapular area included by the pre-scapulars. The post-scapulars are short; by uniting among themselves or their branches they form an irregular plexus. First passing back from the laterals, the pleurals then turn forward at a sharp angle, and, in their course through the middle of the pectorals, send toward the margin a large number of long tubules, each of which bears a small group of branchlets at its end. Connecting with the orbitals by means of a couple of tubules, the pleurals bend back toward the forehead, whence they run forward a little more than half the distance to the tip before descending.

The aural is long and transverse. Starting outward from the aural, the elongate occipitals turn forward, after sending out the occipital branches. In

front of the eye, the short cranials have a very sharp and prominent bend; on the rostrum they are close together and nearly parallel. From the branch sent back of the spiracles the orbitals incline a little outward, and proceed thus until more than half-way to the edge, when they turn inward; close to the rostrals they again take a longitudinal course for a short distance, and find their way down, in front of the pleurals, after sending out upon the fin ten or a dozen long tubules.

On making their appearance on the lower surface the pleurals pass directly forward; nearing the margin they turn and follow it around, gradually receding from it, to a point opposite the mouth, where they turn toward the abdominal chamber. Back of the shoulder girdle they turn slightly outward; and when opposite the pelvis they turn toward it abruptly, meeting the extension from the jugular at the edge of the abdomen. On the transverse posterior portion, near the pelvis, there are a few tubules of medium length; on the portions anterior to the gills there is a multitude of tubules that reach to the edge of the disk. The suborbitals emerge a little in front of the pleurals, which they cross, to run obliquely back until not far in front of the gills, where they take an inward and forward course to meet the angulars a little back of the mouth. As they pass backward they send off nine or ten branches which by repeated forkings and fusions form networks, the outer limits of which are the pleurals, and in which the inner areas are large and elongate polygons and the outer small and short ones. The orbito-nasals are of moderate length, connecting, as in the majority of the Sharks, with the angular and suborbital posteriorly, and with the subrostral and nasal anteriorly. Each subrostral makes a very prominent bend in front of the nostril; it does not return far enough to reach the nasal valve; and it ends at the side of the prenasal, near the skull, in a series of four or five swellings or follicles. No great amount of curvature appears in the nasals. The median is very short. The prenasals are close together and nearly parallel; they have several irregularly placed rings or bunches along their sides. Not far from each angle of the mouth there is a short disconnected oral.

The sketches were made entirely from the left side of the specimen.

This genus is well distinguished from its allies, the Potamotrygons, on the one hand, and the Thalassotrygons, on the other, by the disposition of the tubes on the shoulders, and the orbito-pleural plexus beneath the pectorals.

It is quite possible that the appearance of the follicles on certain of the canals of the ventral surface, attended by deterioration and disappearance of the tubes themselves, in this genus and Urolophus, and in species of other genera, points toward a change made from habits similar to those of the typical Thalassotrygons, in which the lower canals possessed great utility, to others leading the individual to remain habitually on the bottom, where the lower vessels may be comparatively useless, which if persisted in lead to disuse and ultimate obsolescence of the tubes, as in the Torpedinidæ. It is not far to the conclusion that, through their ancestors, Torpedoes, as well as Potamotrygons, were more closely related to the Thalassotrygons.

Urolophus.

Urolophus halleri (Plate XXXVI.). A striking feature in this ray is the absence of the post-scapulars. Their position is occupied by the pleurals and by the pre-scapular branches. In the genera Raia and Rhinobatus the pleural met the anterior of the scapular branches; in this genus it is the posterior. From the anterior part of the scapular curve there is a pre-scapular branch which connects with the scapular, enclosing a small pentagonal area. Behind the aural the laterals converge in a gradual curve until rather close together. The aural is transverse. The occipitals are elongate and diverge forward. At each end of the aural, on the laterals, there is a small occipital tubule with a number of branchlets. The pleurals run forward a little way outside of the basipterygium of the fin; they pass under the suborbitals and go through close in front of the skull. One or more tubules connect these tubes with the orbitals. Laterally long tubules extend more than half the distance to the border. At the fontanelle, the cranials make deep curves outward; beyond this they approach each other until nearly in contact at the tip of the snout. The orbital sinks deeply into the tissue; at the outer edge of the spiracle a tubule is sent backward, farther forward others pass out laterally, one or more uniting with the pleural, and in front five or six long ones reach toward the front edge of the disk. The tube passes down about midway from the fontanelle to the end of the rostrum.

Beneath the disk, on their appearance the pleurals run forward as far as to the middle of the snout; thence they turn laterally and describe an arc of a circle having a radius of about the distance between the first pair of gill openings. This carries them back to a point opposite and near the coraco-scapular, a point from which they pass directly to join the jugular extension. Radiating from the outside of the circle there are two- or four-branched tubules of medium length. Emerging on the lower surface the suborbitals make a broad sweep laterally, then turn back until behind the mouth, and then forward toward the nostril till they meet the subrostrals. The connections of the short orbito-nasal are similar to those of Isurus and the Holocephala, and not to those of the majority of the Sharks. The angular is short, and reaches toward the inner edge of the gill cleft. The jugular bends outward before running back along the branchial apertures. No union is apparent between the rostrals and the subrostrals. From the orbito-nasal the latter are transverse in general course; they make a prominent bend forward in front of the nostril, and another back upon the nasal valve, thence they pass forward at the side of the prenasals, growing more and more delicate and transparent, and vanish before reaching the middle of the snout. Individuals show the peculiar enlargements or swellings in the tubes, in front of the median, that are seen in Potamotrygon. These rings or swollen portions closely resemble the follicles of Savi They seem to be connected with the prenasals by the tissue of the walls, but communication with the chambers of the tubes could not be discovered In the nasals the curves are not very pronounced. The short median is hidden

by cartilage. The prenasals diverge little from the parallel; they are disconnected forward. Behind the mouth, on each side, is a disconnected oral.

The tubules of the back are more or less dissected into fine branchlets, which form small groups about the ends. On the head the branchlets are close together. Only the principal ones were sketched, but, when possible, they were followed to their terminations.

Urolophus torpedinus differs from *U. halleri* mainly in matters of detail, in tubules, etc. The specimen at hand has five of the enlargements, at the side of the prenasal, in the subrostral; the tube ends with the fifth, seemingly without other anterior connections, excepting by tissue from the walls.

The junction of the pleurals to the anterior scapular branches in Rhinobatus, and to the posterior in Urolophus, indicates that both may have been secondary attachments; in other words, that the attachment of origin in the pleural is that with the orbital

Tæniura.

Tæniura lymma (Plate XXXVIII.) possesses both pre-scapular and post-scapular branches. What is called the pre-scapular area in Urolophus and in Dasybatus becomes, by the junction of the pleural tube to the middle of the outer boundary, a scapular area in this form. Three of the long tubules on the hinder part of the pectoral diverge from a single short stem, which connects them with the pleural. After connecting with one or more of the orbital tubules, the pleurals go downward near the forehead. Immediately in front of the prominent scapular curve the laterals approach each other closely. They send out the occipital branch near the end of the aural. Along the greater portion of their lengths they are studded with short tubules, the majority of which are branched two or more times, making four or more of the branchlets. On the skull the extremities of the dissected tubules interfere with each other so much, and become so confused, that it is not possible to present more than an approximation in the sketch.

An arrangement of the pleurals on the under surface intermediate between that of Urolophus and Dasybatus is presented by this specimen. The lateral curve of the tubes is not so round or so regular as in the former genus, and the tubules are more massed along the anterior edge. Compared with the latter, the lateral sweep is more regular, and the tubules are much less crowded along the anterior margin. From their point of appearance near the median the pleurals describe curves which are entitled to rank as intermediates between those traced by the same tubes in the genera cited. At each end the suborbital is bent so as to form a hook; it meets the angular. Forward from the nostril there is a deep fold in the subrostral; the tube does not return quite to the nasal valve, and it cannot be traced beyond the base of the snout. The nasal is moderately curved. There is a very short median, apparently transverse. Behind each side of the mouth there is a short oral, which has the appearance of being affected by the swellings elsewhere seen in subrostrals

or prenasals, possible precursors of the follicles of Savi, evidences of the action of causes tending toward disruption and destruction of the canals. Below the disk the tubules are rather short and are somewhat separated, but not so much so as in Urolophus.

The great difference of the canal distribution as compared with that obtaining on the Potamotrygons is evidence to be added to that advanced by the writer in 1877, of the necessity of separating the river Trygons from the species properly belonging to the genus Tæniura.

Dasybatus.

Forward on the thoracic region of *Dasybatus nudus* (Plate XXXIX.) the laterals are nearer to each other than they are above the abdomen. On the shoulder the curve is moderately prominent. There is a pre-scapular branch, and also an area. There are no post-scapulars. The pleurals do not extend much farther out than the basipterygia of the pectorals; their tubules reach more than half-way to the margin of the disk, and end in small groups of branchlets. The pleurals descend rather close to the forehead. The aural is moderate; the occipitals are longer; and the occipital branches may spring either from the occipitals themselves, or from the laterals, or from both, as may happen, though most often they appear on the first. Posteriorly the cranials converge; the orbital curve is pronounced; and the canals seem to end on the snout. The orbitals cross the pleurals twice; they then go through to the lower face of the disk, more than half the length of the rostrum from the forehead. Their tubules are long and are branched at the ends. One only joins the pleural.

Under the disk the figures outlined by the tubes are still more characteristic. Within the subrostral loop, in front of the nostril, the pleural makes its appearance. From this point it sweeps out and forward toward the tip of the snout, crossed by the subrostral once and by the suborbital three times. Before reaching the extremity it turns, and, running close along the anterior margin, sends forward a great number of fine short tubules. Near the outer angle of the pectoral it bends across the fin toward the pelvis, in front of which it meets the post-jugular extension. All of the tubules on this surface are along the pleural in front. Four areas are outlined by the suborbital. Only one of them is completely circumscribed by it, from the fact that two of its branches end without connections. With the aid of the pleural, in front, the otherwise open areas one, two, and four are enclosed. The first goes back as far as the nostrils, the second as far as the mouth, the third as far as the middle of the space between the mouth and the gills, and the fourth area ends opposite the second gill opening. Suborbital and subrostral meet at the short orbito-nasal. Angular and jugular are both crooked in irregular flexures. The subrostral is very much bent and folded; a prominent loop extends forward in front of the nostril, and another upon the nasal valve. This canal disappears, without visible connections, at the base of the snout. The nasal has not a

great deal of curvature. The median is short. The prenasals are long. On each side of the middle behind the lip is an oral that extends but little farther than the corner of the mouth.

Marked variation in the branches of the suborbital occurs on the specimen sketched. Of species similar in shape, *Dasybatus walya* resembles this one very much in the patterns described by the orbitals, but *D. zugei* is even more simple than *D. dipterurus* in respect to the same tubes. In the first case cited the similarity is so close as to raise doubts of the specific distinction of the two.

Dasybatus dipterurus (Plate XL.). Compared with the preceding, this species shows less prominent scapular curves, sharper bends in the cranials, more connections between orbitals and pleurals and less distance between their points of descent, and a larger number of tubules. On the lower surface the differences are a great deal more pronounced. The pleurals do not reach so far laterally, and they bear tubules toward the sides and posteriorly as well as in front. The suborbitals traverse a comparatively direct course, though affected by many small flexures, till they reach a point opposite the mouth, where they turn toward the nostrils, parallel with their former route, and meet the subrostrals directly in advance of the first gill cleft. The subrostrals also are sinuous; they form a prominent loop in front of the nostril, and, apparently, vanish near the base of the rostrum after advancing very little on the nasal valve. There is little doubt that the subrostrals and rostrals join; the latter pass to the lower surface, and may be traced back half the length of the snout before the walls of the tubes become so thin and delicate as to be undistinguishable from the surrounding tissue. The condition of the orbito-nasal in this specimen is one of uncertainty: on one side the subrostral and the orbital meet, on the other side the subrostral and the nasal join.

Dasybatus tuberculatus (Plates XLI., XLII.). Differences between this species and the preceding are numerous, and very noticeable. But a moderate degree of prominence is to be seen in the scapular bends of the laterals. The scapulars and the pre-scapular area are separated. The occipital branch is situated at the end of the aural. An intricate orbito-pleural plexus is formed, in which the spiracular branch of the orbital is concerned, with the usual anteorbital tubules. The tubules are abundant, elongate and branched; the posterior one on each pleural is forked. Toward the forehead the cranials diverge gradually; opposite the fontanelle the curves are strong and sharp. Half-way from the eyes to the end of the snout the orbitals pass to the lower surface. On the same transverse line, below the snout, are the points of emergence of both the orbitals and the pleurals, the latter being a trifle farther from the prenasals, although on the top they started down close to the skull.

Considerable resemblances are seen in the outlines traced by the pleurals on the ventral aspects of the three species sketched, from this genus. There is the same outward prenarial curve, the same course along the anterior border with the great number of short tubules, and a similarly crooked route across the pectorals in the direction of the pelvis. The suborbitals connect with the

subrostrals, as in both of the preceding, but do not reach them by a comparatively simple course, as in *D. dipterurus*, or through complex areas, as in *D. nudus*. At the start they run forward to turn sharply back and to the side, before reaching the pleurals; then they commence a series of perplexing and seemingly erratic turns, doublings, and zigzags, that ultimately bring them opposite the second gill clefts and thence forward to the short orbito-nasals. Equally crooked is the course of the subrostral; it makes two prominent loops at the side of the nostril, one in front of it, and another at its inner side upon the nasal flap, before making its way directly to meet the rostral at the tip of the rostrum. The nasals partake slightly of the tendency toward sinuosities, as also the prenasals, orals, angulars, and jugulars. The median is short.

No attempt has been made in the drawing to follow the tubules of the head or back. The laterals continue along the sides of the tail throughout the whole of its great length. Under the snout the subrostral is difficult to trace, so much so that the connection with the rostral may yet be considered an open question.

Pteroplatea.

Plates XLIII.–XLV.

Nowhere else in the order, so far as it has come under our notice, does the development of the canal system attain such a degree as in this genus. So great is the number of tubules and branchlets that the larger portion of the upper surface is a tangle of minute vessels. They are most closely grouped in a broad band along the anterior margin, and on the head; posteriorly they are not nearly so much crowded. A space entirely unoccupied by them is found on the middle of each pectoral, whence it extends upon the branchial area. Smaller spaces, quite as free from them, appear in the scapular areas, and above the abdomen behind the scapulars. On the ventral surface the extent of the canals is not so remarkable; it is not much greater on this side of the disk than in species of Dasybatus. The only cause that suggests itself for such an extraordinary development of the system on forms that seem so poorly provided with means of progression, of defence, or of procuring subsistence, is a greater dependence on vibrations in the water for knowledge of the presence of enemies or of prey.

Pteroplatea hirundo (Plate XLIII. fig. 1). Resemblances in shape of disk between this species and *P. valenciennii* are accompanied by similarities in the figures outlined by the main canals. The pre-scapular area is large, and lies in front of a scapular network, in the formation of which the post-scapular is also con d. Anteriorly the smaller canals are less numerous and much more loosely arranged than in either of the following species. Posteriorly, also, the vessels are less abundant, and their general appearance is more straggling and scattered than the case on the same locality in those forms. The pleural appears on the lower surface about half-way from the median to the tip of the snout.

Pteroplatea marmorata (Plate XLIII. fig. 2). Greater length of disk and less lateral extension naturally bring about differences between this species and the following, in regard to shapes and outlines of areas, etc. For instance, the curve in the pleural behind the shoulder is comparatively deeper and shorter, and the finger-like area, projected toward the outer angle, stretches obliquely backward instead of nearly straight outward.

A pair of strong pre-scapular branches are situated close together on the forward portion of the scapular curve. These are not connected with the scapular area, which is at some distance from them and close to the pleural canal. An elongate post-scapular branch lies near to, and for some distance parallel with, the pleural. The masses of tubules and branchlets are more compact than in the preceding, and less dense than in the following. On the lower surface the pleural emerges two fifths of the distance from the median to the tip.

Pteroplatea valenciennii (Plates XLIV., XLV.). Neither of the other species figured possesses so great a number of tubules as this one. Forward, the tubes are completely hidden. The laterals may be traced without removing the smaller vessels, except close to the back of the head. In the scapular section the curves are extensive, though not very prominent toward the pectoral. Near the aural the tubes are rather close together; from their bends in this vicinity long tubules, with two or more branches, extend back beyond the shoulders. Long tubules, also, put out from the sides of the laterals over the abdominal chamber, beyond which the main canals continue to the end of the tail. A couple of pre-scapular areas lie in front of the scapulars; the latter originate in a plexus of scapular and post-scapular branches, in which it is difficult to trace the main line. A broad shallow bend, toward the hinder margin, brings the pleural behind and outside of the middle of the pectoral; there it turns forward and slightly inward till in front of the middle, where it turns directly toward the outer angle, making a deep notch, open backward. Some distance from the angle of the fin the tube turns toward the eye, nearly parallel with the margin, and, after meeting four or five of the suborbital tubules, descends near the forehead between the suborbital and the cranial. Anteriorly the tubules are numerous, branching into a thicket; posteriorly they are not so many or so short, and do not present such a confused mass of branchlets. Occipital branches occur on both laterals and occipitals. Opposite the orbits the orbitals make a prominent bend outward. On this bend are the tubules connecting with the pleurals; behind it are several long branches; and in front of it are a number of long tubules reaching forward. The orbitals descend in advance of the pleurals, and much nearer the rostrals. On the cranial the ante-orbital curve is sharp and produced.

Ventrally the pleurals extend near the front edges of the pectorals, for more than two thirds of the length of the latter, before turning toward the abdomen and meeting the jugular extension a little backward from the scapular arch. They emerge in the posterior third of the distance from the median to the tip of the snout; not as shown in the sketch, where the median is too far back and the pleural too far forward. The orbito-nasal is a mere point, as if the tubes

crossed each other at right angles. For about half the width of the pectoral, the suborbital passes directly outward, parallel with the pleural. From its outermost point it goes to the orbito-nasal. The subrostral lies close to the side of the prenasal, connects with the rostral, and does not reach the nasal valve. The median is short. The prenasals are moderate, disconnected in front. The pleural tubules of this surface, the lower, are most numerous on the anterior section of the tube; they are not long, and have no branches

Myliobatis.

Plates XLVI.-XLVIII.

Above the disk the canals and their branches extend only about half-way from the vertebral line to the outer angles of the pectorals. Within these limits the surface is closely occupied. There is a great tendency to form rosettes or mats of branchlets, at the ends of the tubules. From the forehead back to the base of the tail on each side of the vertebral column, the groups are dense, and so large as to be nearly continuous as a single one. The pleurals range close to the borders of the branchial areas.

On the lower surface the pleurals run outward and return near the anterior border of the pectoral, and they then pass backward very near the basal cartilages, thus merely skirting the fin. Elongate tubules pass outward on the base of the fin, hardly covering a fourth of the length, and others pass from the jugular extension inward upon the abdomen. In great part the orals are longitudinal. A continuous tube has, in each of the species drawn, taken the place of the separated sections of the oral, as apparent in the majority of the Batoidei.

Myliobatis aquila (Plates XLVI., XLVII.). Tubules and branchlets are numerous, above the abdomen, on both inner and outer sides of the laterals, in this species. The scapular curves are not very prominent; the scapular angle is sharp. A pre-scapular enclosure, of moderate size, lies in front of the scapular, and, by union of pleural and the elongate post-scapular branch, a small scapular area is enclosed. The branchial area is somewhat well covered by mats of branchlets, from the occipital and from the pre-scapular tubules. The occipital is elongate, and in some cases it bears the occipital branch; in others, this branch rises behind the aural. Tubules are very plentiful on the cranials. The ante-orbital bend in these tubes is moderate, and their rostral portions are short. Near the spiracle the orbital crosses the pleural, and it traverses two thirds or more of the length of the snout before going to the lower surface. In front of the eye the pleural rises upon the forehead; it makes its appearance on the under side near the nostril. Pleurals, orbitals, and cranials are thickly beset with tubules on or about the skull.

Beneath the disk the outward course of the pleural lies near the anterior margin, for two thirds of the length of the latter; the tube then turns back, making a sharp angle, to take a backward course close to the jugular. It does not extend as far back as to the pelvis, and the spaces enclosed by it, with the jugular and suborbital, are very narrow and elongate.

Behind its junction with the orbito-nasal the elongate suborbital makes a prominent loop. A similar loop occurs in the subrostral in advance of the nostril, and a second appears between the nostril and the median. The nasal is not greatly curved; it joins the subrostral, which in turn unites with the prenasal. Median and prenasals are short. The oral is crooked and branched; it extends back between the branchial clefts of the first pair. Tubules of moderate length, more or less branched, reach out upon the abdomen from the jugular, and upon the posterior areas of the pectoral fin from the pleural.

Myliobatis freminvillei (Plate XLVIII.). Compared with the preceding this Ray has a greater number of the pleural tubules massed together opposite the spiracles, and fewer of them reaching out upon the body of the fin; and it has longer rostrals, orbitals, and prenasals. The scapular enclosure appears incomplete on its outer boundary. The occipital branch is connected with the long occipital, and also with the lateral, possibly an individual peculiarity. Beneath the disk the areas enclosed by the pleural are more irregular, but the oral is curved much more regularly. The nasal joins the subrostral, which unites with the rostral. The orbito-nasal is short, being little more than a crossing of nasal and angular. Subrostrals and prenasals are not united.

Aëtobatus.

Aëtobatus narinari (Plate XLIX.) has but slight scapular bends in the laterals, and, apparently, has neither pre-scapular areas nor pre-scapular branches. A post-scapular branch or two enclose a very small space. On the pleurals there are few branches; those that exist are long, reaching beyond the middle of the fin. The branchings of the tubules are similar to those of Myliobatis and its allies. Opposite the end of the aural on each side is an occipital branch. The occipital is long. A spiracular branch was not discovered on the orbital. For a short distance this tube unites directly with the pleural, without the intervention of tubules, as in most Batoids; it crosses the track of the cranial twice, in front of the skull, and it descends not far from the tip of the rostrum. The pleurals descend much nearer the fontanelle.

The arrangement of the lower pleurals is similar to that of Myliobatis, though the canals extend farther outward or backward; they are hardly so close together in front, but are closer to the jugulars along the branchial clefts. From both of the transverse lines of the pleurals, near the forward edges of each pectoral, the tubules run toward the front; from the longitudinal portions of the same tubes they pass outward, and from the hinder part of the extension from the jugular they reach inward. The suborbital and the angular meet below the posterior edge of the orbit, whence a long orbito-nasal connects them with the nasal and the subrostral. Both of the curves in the subrostral, that in front of the nostril and that on the nasal flap, are sharp and prominent; the tube joins directly with the prenasal a little way in front of the median. As is generally the case in the group, the median is rather short; the point at

which the nasals unite is vertically above, or a little in front of the mesial forward bend, formed by the junction of the prenasals with the median. Consequently the median may be described as nearly or quite vertical. The prenasals are elongate; they unite directly with the subrostrals, forming with them a single tube on each side of the rostral cartilage, as in *Myliobatis aquila*. In *M. freminvillei*, which more closely resembles Aëtobatus in shape, these tubes are closely applied, but remain separate. At each side of the median line the oral of Aëtobatus sends forward a sharp curve, and on the outside of each of these a similar loop is sent outward; the tube goes some distance backward from this second bend before turning outward and forward. It ends without joining the angular.

The closeness of the relationships existing between this genus and the preceding are asserted in the characteristics of the canal system with as great emphasis as in any other portion of the anatomy.

Rhinoptera.

Plates L., LI.

So far as the general features of the canal system are concerned, this genus resembles both of the preceding. At the same time there are respects in which it differs decidedly from either of them. The majority of these are due to difference in the structure of the head, yet the divergences are not wholly confined to this portion. Again, on comparison with Dicerobatus the indications of close affinities are very conspicuous on the trunk, but on the head the relationship becomes apparent only on closer study, being masked by the dissimilarity in shape.

Rhinoptera brasiliensis (Plate L.). Abrupt bends give the scapular fold in this type more prominence than it would attain by a gradual curve, as it departs but little from the main course of the lateral. This fold bears a pre-scapular and also a post-scapular branch, and between them an elongate pre-scapular and a much smaller scapular inclosure. Behind the end of the aural, on the lateral, there is a strong forked occipital branch with a multitude of branchlets. Leaving the scapular area the pleural goes back and outward a short distance, where it has the appearance of being crowded back upon itself in a number of folds; from these it extends with tolerable directness to the side of the head. Its branches are few and long; their ends are much dissected. The two tubules in front of the posterior one are forked near the middle of their length; the hinder one branches a greater number of times.

All of the anterior cephalic canals are affected by many flexures, as if in compensation for the short distances between the extremities of the tubes. Bringing the mouth so far back toward the gill-openings, and ending the snout below the forehead, gives the rostral canal a vertical direction, and carries orbital and pleural under the anterior part of the skull. The tubules of the orbital pass forward on the inclined portion of the forehead. No distribution of the canals occurs on the upper surface of the rostral fins; the tubes seek the

lower face, going between these fins, and there become more sinuous and make broad and sweeping bends.

At the side of the head, opposite the angle of the mouth, angular, pleural, and suborbital are close together and paraHel. Below, the pleural emerges farther back than its point of disappearance on the top. It passes to the side of the face, thence to the pectoral, where, in its outward and its inward course, it traces a pair of lines along the greater part of the anterior border of the fin. Returned from this it runs back nearly parallel with and not far from the jugular extension toward the pelvic region. The tubules of both the anterior lines are directed forward; of the two posterior lines those of the outer line are extended outward, and those of the inner toward the abdomen, inward. Passing around on the rostral fin, near its border, the suborbital reaches a point on the side of the head, near the corner of the mouth, where it accompanies the pleural while making a long loop outward; coming back from this, it unites at once with the angular. The orbito-nasal is long, curving toward the oral. The nasal itself is neither long nor greatly curved. Two great loops occupy the whole of the subrostral: one turning forward in front of the nostril, and the other backward upon the nasal valve. Both the median and the prenasals are short. The latter are not connected with the rostrals. Behind each side of the mouth there is an oral of moderate length, in which the ends extend transversely in opposite directions from a median longitudinal section.

Rhinoptera (*Zygobates*) *jussieui* (Plate LI.). Prominent among the features in which this species differs from the preceding are the increase in the number of tubules on the cranials, the presence of a group of tubules immediately behind the orbital on the occipital, the extension of the prelateral branch between the spiracle and the cranial, the shapes of the scapular and the pre-scapular areas, the augmented number of branches on the posterior scapular tubule, the more regular curves in the suborbital and the subrostral, and in the union of the oral across the median line. Besides these there are other particulars of variance, more or less important, as a smaller amount of curvature in the pleural tubules of the ventral series, and greater parallelism in the prenasals, seen on comparison of the drawings. A close relationship of these species is indicated by the many points common to both.

Dicerobatus.

Dicerobatus olfersii (Plates LII., LIII.) presents a distribution of the corporal canals that, in the main features, bears much resemblance to that of Myliobatis, Aëtobatus, or Rhinoptera. There is a similar nearly parallel arrangement of two sections of the lower pleural near the front margin of each pectoral, and of two others, closer together, along the basipterygia of the same fin. On the dorsal surface the likeness to Rhinoptera is the greater. At the shoulder there is a single large pre-scapular area. Near the scapular arch the sinuous folds of the pleural are less prominent than in the preceding, but the branchlets of the tubules are even more massed toward the posterior angle of the fin. A post-

aural branch on the anterior extremity of the lateral recalls the same feature in Rhinoptera. Apparently the number of branchlets and openings is greater in Dicerobatus than in either of the other genera cited, and they form closer aggregations along the laterals or over the head. Connection between the laterals, across the vertebral line in the vicinity of the shoulder girdle, has not hitherto been observed. Still greater differences exist in the cephalic canals. If a specimen of one of the species of Rhinoptera were to have the pre-oral fins separated along the median line, and their inner edges carried upward and outward so as to be united to the skull along the edge below the eye, the mouth being at the same time much widened, an arrangement of the canals might be brought about that would present a somewhat near approach to that obtaining in Dicerobatus, so far as the distribution of the main vessels is concerned. The affinities between these genera are well indicated in the canals.

Laterals. — From the aural each lateral passes obliquely outward to the post-aural branch; thence it takes its way toward the point of junction of shoulder girdle and vertebral column. Nearing the latter, it sends a couple of tubes across it to the lateral of the opposite side, and immediately behind them turns inward and around, under itself, so as to make a rounded loop just in front of the pre-scapular enclosure. This may be an individual peculiarity. Behind the area the pleural is met, and farther back numerous tubules are sent out toward the median line. Half-way to the tail, or farther, some of the tubules pass to the outer side of the canal. In front of the shoulder seven or eight tubules are sent inward toward the vertebræ. The greatest branches are the post-aural and the scapular branch, by which the scapular area is enclosed.

Pleurals. — Each pleural encloses a branchial area of moderate size, that is widest near the middle of its length and pointed toward each end. Twenty-four branches pass outward from the canal, in the specimen at hand; the median reach little more than half-way from the middle of the back to the tip of the pectoral. The posterior of these tubules are more branched than the anterior, the latter being short, confused, and irregular. To make its descent to the lower surface the pleural passes through the edge of the disk, a short distance behind the spiracle, and drops downward, meeting on the way several tubes connecting with the orbital, until below the level of the eye, where it turns forward nearly parallel with, and a short distance below, the suborbital. With the latter it is connected at narrow intervals by short tubes, a half-dozen or more in number. Below the pleural, in the suborbital region, there are about a dozen short tubules with numerous fine branches, the openings of which appear as thickly strewn dots on the surface. Some of these tubules originate in the pleural, the majority, however, belong to the suborbital. A little distance in front of the eye the pleural passes obliquely backward and inward to the lower surface, making its appearance a very little in front of the nostril. From this its course is somewhat irregular backward and outward to a point below the spiracle, whence it turns still more outward and upward toward the lower side of the pectoral near the anterior border. Oppo-

site the angle of the mouth three or four tubules are sent downward and forward toward the lower border of the cephalic fin; a couple are sent inward behind the mouth; and several short ones are extended inward just before the tube enters its outward course along the border of the pectoral. Toward the anterior margin of this fin the canal puts forth a large number of short tubules, and near the outer angle, at the point of turning back on itself, two elongate branches are extended toward the tip. Each of these branches bears tubules. Returning toward the mouth the course of the pleural is not much farther from the edge. At first after making the bend it sends several tubules forward, then, near the middle of the fin, a number turn backward; nearing the first gill opening, some start forward, but turn and cross the canal, and still nearer, before turning back by the side of the extension of the angular, a few irregular branches are pushed forward. In their backward track the two inner sections of these sub-pleurals lie close together. The outer of the two has by far the greater number of tubules; from the shoulder girdle, anteriorly it sends these outward; near the girdle they are turned inward to cross the inner tube and reach the abdominal region. Opposite the middle of the abdomen, near the end of the course, the majority of the branches turn out and backward; a few only turn in to cross the tube; and at the turning-point of the tube an elongate tubule goes back upon the ventral fin. As the canal goes forward toward the jugular, it bears several branches turning toward the ventral region, then a few that cross the other section of the tube outward; but after leaving a point opposite the middle of the belly, it bears no others.

Aural. — This tube is elongate and strongly bent back in its middle, behind the openings of the aqueducts. Near the median line it sends back three or four tubules.

Occipitals. — From the aural, each of these tubes extends toward the eye, at the same time making a broad curve toward the branchial area, and sending several irregular branches in the same direction.

Cranials. — A cranial goes forward from the end of each occipital directly toward the tip of the outstretched cephalic fin, without passing beyond the skull. Posteriorly each bears a number of tubules reaching toward the median line, but beyond a third of the distance forward they all reach outward to the supraciliary prominence, where they end in a band of thickly set punctures. Anteriorly the tubules are more numerous, more slender, and more crowded.

Rostrals. — The rostral turns rather abruptly back and inward from the end of the cranial. It runs near the front edge of the snout until about half-way to the median line, where it passes to the lower surface. On the under side of the snout it curves broadly in the direction of the prenasals, then, taking a lateral direction before reaching the mouth, crossing and recrossing the nasal, and making a bend forward in front of the nostril, it crosses the pleural before meeting the orbito-nasal, which it joins opposite the corner of the mouth. One of the rostrals (*sr*), that on the right side of the specimen dissected, appears to be abnormal; it crosses the pleural, and a short distance behind it stops abruptly, making no connection whatever.

Orbitals. — The junctions of orbitals and cranials are deeply buried in the tissues of the top of the head. The orbital is directed obliquely out toward the eye. In front of the spiracle it passes through the cartilage to the side of the head; there it makes a shallow backward curve and meets three or four tubes connecting it with the pleural. Eight or ten similar connections are made from the suborbital, behind the point at which it is crossed by the pleural, as the latter passes to the lower (inner) surface between the fin and the skull. The majority of the branches uniting with the pleural below the suborbital in reality originated in the suborbital, but in crossing the other tube have become joined to it. After being crossed by the pleural, the suborbital, on its way forward, makes a number of sinuous windings, and sends forth a number of strong many-mouthed tubules, which are nearly parallel as they reach ahead. Anteriorly the tube divides. One section of it passes the edge of the fin to take a course on the inner side along the margin toward the tip; near the latter it turns back, in a slightly sinuous track along the middle of the inner surface of the fin, crossing the pleural, and meets the angular some distance behind its junction with the subrostral. The other section of the suborbital turns toward the rostral, running between it and the edge of the snout. Apparently it connects with the rostral, not far from the cranial, and descends, without going as far toward the median line as the former, to meet the extremities of the prenasals. The connections and extent of this portion of the suborbital are subject to a little uncertainty on account of the number, excessive delicacy, and confused condition of the tubules, and the preclusion of injections by the preservation of the specimen. The openings of the branchlets of the suborbital form an elongate band of pores extending below the eye forward to the upper edge of the fin.

Nasals. — These are strong transverse tubes; they become calcified as they approach the median.

Median. — This tube is elongate, transverse, and, like the nasals, enclosed in a calcified envelope.

Prenasals. — These are of moderate length, calcified posteriorly, delicate and slender anteriorly, and, apparently, connected in their front extremities by a very slender vessel from the suborbital and rostral.

Orbito-nasals. — The orbito-nasals are of considerable length, and turn outward posteriorly.

Angulars. — Each angular makes a broad outward curve toward the front margin of the pectoral.

Orals. — Excessive fineness and delicacy in these vessels makes it very difficult to work them out. They were first sketched from the low ridges formed by the canals on the outer skin. The terminations and finer branchlets, of course, could not be marked in this manner. On removing the skin, however, some of the tubules were lost, and it was found better to give the sketch as taken from the surface.

HISTORY.

The mucous ducts and the canals were more or less confused by the earlier writers. Usually both systems were treated as apparatus for the secretion of mucus, and for distributing it over the skin. It was a long time after the structural differences were pointed out before the difference in function was recognized. On account of the confusion, the list of authors treating of the canals is made to contain also those treating of the ducts, as there are in most instances contrasts with the canals, or references to them, even in such writings as are most exclusively devoted to the ampullæ of Lorenzini. And, further, to make the literature approximately complete on the embryogeny, the innervation, and the general homologies of the system, it is found necessary to include studies of similar organs on the Fishes, the Batrachia, and the Insects. Consequently a few works are cited which have indirect connection only with the subject of this paper.

As early as 1664 the outward openings of the ducts on the skin of the Skate were noted by Stenonis. Those on one of the Sharks were described by him in 1669. The information given by Blasius, in 1681, was drawn from the publication of Stenonis.

Lorenzini, 1678, in observations on the Torpedoes, recognized the existence of the two classes of vessels, and distinguished them by their distribution and by their branchings. Following the ducts he discovered their swollen inner terminations, now called the "ampullæ of Lorenzini."

Monro, 1785, in his book on the "Structure and Physiology of Fishes," figured both ducts and canals. Plate V. of his work traces the canals on the head and shoulders of a Cod. Plate VI. exposes the ventral ducts and the canals of a species of the genus Raia; and Plate VII. shows the ducts of the upper surface of the same Skate. According to this author each system formed part of "a very elegant structure for the preparation of the mucus."

Geoffroy, 1802, published his opinion that the mucous ducts of the Skate were the analogues of the electric apparatus of the Torpedo. His conclusions did not meet with ready acceptance among his contemporaries.

Jacobson, 1813, put out a short paper, entitled "Extrait d'un Mémoire sur un organe particulier des sens dans les raies et les squales," in the "Nouveau Bulletin des Sciences, par la Société Philomatique de

Paris," VI., p. 332, in which he announces the discovery that the ducts are organs of sense, carrying vibrations from the surrounding water to the nerves. He also pointed out that these vessels could hardly be the analogues of the batteries, both being found in the Torpedoes. Treviranus, Knox, and others followed, agreeing more or less completely with his conclusions. Delle Chiaje, Savi, and other observers, still claimed that the ducts were to be regarded as "organi mucipari," distributing the slime over the surface.

Blainville, 1822, and others of his time and later, among them Müller, looked upon the canals as apparatus for the secretion of mucus.

Savi, in 1840, announced his discovery of the "appareil folliculaire nerveux" to the Scientific Congress at Florence, and a year later it was published in the "Atti della terza Riunione degli Scienziati Italiani in Firenze."

Mayer, 1843, arrived at conclusions similar to those of Geoffroy, 1802, and held that the mucous ducts of the Raiæ were the analogues of the electric batteries of the Torpedinidæ.

Savi, 1844, sent out his "Études anatomiques sur le Système Nerveux et sur l'Organe électrique de la Torpille," in Matteucci's work, "Traité des Phénomènes Électro-physiologiques des Animaux," of which it forms an appendix. Here he gives a detailed description and figures of series of follicles on the Torpedo, which are apparently of the same character as those sketched in the present work, on Discens, Potamotrygon, and Urolophus, and which are here proved to be part of the canal system.

Without mentioning all the writers who may have touched upon, or referred to either canals, follicles, or ducts, we may simply call attention to Wagner, 1847, to whom is to be credited the hypothesis that the function of the follicles of Savi is to excite the activity of the electric organs, and then proceed to several of the more important contributions toward an understanding of one or another of the organs.

H. Müller, 1851, makes three groups of the vessels, the greater part of which are to him organs of sensation instead of secretion. To quote his words, "Unter der Rubrik 'Schleimkanäle' sind bei den Knorpelfischen verschiedene gebilde zusammengefässt, von denen nur ein Theil den Schleimkanalen der Knochenfisch analog ist. Ein grosser Theil der Kanäle bei Knorpel- wie bei Knochenfischen hat bestimmt nicht Secretion sondern Sensation zum Zweck."

Leydig, 1852, also makes three classes of the vessels, one class including the ducts, another the canals, and another the follicles of Savi. He characterizes them thus: —

"1, als verzweigte Röhren, die in oder unter der Haut liegen. Sie setzen zusammen das System der Seitenlinie also die Seitenlinie selbst und ihre Ausläufer;

"2, als nicht verzweigte Röhren, welche mit einer erweiterung — Ampulle — blind geschlossen beginnen und sich auf der äusseren Haut öffnen;

"3, als geschlossene Blasen, die also nicht in der Haut ausmünden.

"Mit der ersten und zweiten Classe sind sämmtliche Rochen und Haie versehen, mit der ersten, zweiten und dritten zusammen bloss die Zitterrochen."

Kölliker, 1856 and 1858, and Max Schultze, 1862, showed the existence of a sensitive epithelium within the follicles.

Leydig, 1868, brought forward one of the most important contributions to knowledge of the organs under consideration. It was entitled "Ueber Organe eines sechsten Sinnes," and it deals with the matter in the most comprehensive way. The three classes of vessels are accepted as organs of a sixth sense.

Boll's monograph, "Die Lorenzinischen Ampullen der Selachier," appeared in the same year, 1868. As its name indicates, it was devoted to the ducts, but references to the canals are included.

A valuable addition to the literature, and very exhaustive so far as the follicles themselves are concerned, is the monograph, "Le vesicole di Savi della Torpedine," 1875, by the same author. He is able in this work to give no additional light on the physiological function of the vesicles. The idea that they are a form of the canals has little in it that is seductive to him, since it involves, as he says, ascribing one office to two organs of very different structure in the Selachia generally, or to three diverse organs in the Torpedinidæ alone. The hypothesis of R. Wagner, that the follicles provoked, in reflex manner, the activity of the electric organ, he claims to have shown in 1873 to be without foundation; and he maintains that the opinion that the follicles of Savi represent an organ of electric sense may only be discussed when the presence or absence of analogous organs is established in the other electric fishes.

To Balfour, 1878 and 1881, more perhaps than to any other one, we are indebted for knowledge of the origin and innervation of the canals. He first found the lateral nerve to originate as the other nerves, and to push backward, following the lead of the canal and sending branches to connect with it in the successive segments that were traversed. His conclusions disagreed with those of Semper and Goette, who claim that the lateral nerve originates directly from the epiblast of the lateral line, but the results of more recent study favor his opinions rather than theirs.

In connection with the embryogeny, segmental distribution of the nerve-endings, etc., it is found necessary to refer to a number of publications relating mainly to other organs of the Selachia, or to similar organs in other classes of animals. Semper, Goette, Eisig, Dercum, Van Wijhe, Hoffmann, Wright, and others, have all put forward contributions which may not be overlooked, though not in most cases directly connected with the subject of this paper.

Solger, 1878–80, is the author of a number of papers relating to the microscopical anatomy in Selachia, Holocephala, and Fishes.

Sappey, 1880, in his "Études sur l'appareil mucipare et sur le système lymphatique des Poissons," did some work on the Selachia, the results of which are indicated on several plates illustrating the courses and connections of the canals, as well as of the mucous ducts, of a Skate, probably *Raia clavata*, and of a Shark, probably Galeus. This is the nearest approach to a delineation of the canal system since the attempt of Monro, nearly a century previous. Some peculiarities are to be seen on the plates in Sappey's publication, which apparently make the species dissected for the drawings to differ greatly from others of their genera. A number of the items of greatest variance are evidently the consequences of incomplete observations. The most questionable points on his Skate are these: (1) the connection of prenasal and subrostral; (2) the absence of connection between subrostral and rostral; (3) absence of junction of suborbital and orbital; (4) the disunited condition of upper and lower sections of the pleurals; (5) the ending of the upper pleural near the orbit; (6) the presence of a transverse canal between the cranials in front of the orbital; and (7) the absence of the aural. On his Shark neither aural, orbitals, nor orals would appear to have been discovered.

De Sède, 1884, in his "Recherches sur la ligne latérale des Poissons osseux," details the results of a number of essays toward a determination of the uses of the organ. In this work he also instituted a number of comparisons for the purpose of ascertaining its value in classification. He occupies the position of a pioneer in the directions of his study. From his experiments he decides that the line is a tactile organ of extreme delicacy. In the Selachia the canals demand higher rank as aids in classification than he accords them in the Teleostei, and his conclusion that the apparatus is more necessary to the least migratory fishes is directly opposed to what is seen on such Sharks as Alopias, or such Rays as Dicerobatus.

Beard, 1885, has made one of the most recent and important contri-

butions to the literature of the subject. In the main, his conclusions agree with those of Balfour.

Though the distinctions between the canals, the ducts, and the follicles had by a number of writers been kept prominently in sight for many years, Professor Agassiz was the first to attempt the use of the canal system as a basis for homologies, as an aid in classification, or as a means of tracing affinities, purposes for which it is admirably adapted.

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LIST OF PLATES.

ABBREVIATIONS.

ang.	Angular.	*n.*	Nasal.	*pp.*	Post-pleural.
au.	Aural.	*o.*	Oral.	*r.*	Rostral.
cr.	Cranial.	*oc.*	Occipital.	*sc.*	Scapular.
g.	Gular.	*on.*	Orbito-nasal.	*so.*	Suborbital.
j.	Jugular.	*orb.*	Orbital.	*sp.*	Spiracular.
l.	Lateral.	*p.*	Pleural.	*sr.*	Sub-rostral.
m.	Median.	*pn.*	Prenasal.	*st.*	Sternal.

PLATE

I. *Isurus punctatus* sp. DeKay. With the names and abbreviations. Fig. 1, top, 2, front, 3, lower, and 4, side view of head.

II. *Chimæra monstrosa* Linné. Fig. 1, side, full length; 2, top, 3, front, 4, side, and 5, lower view of head.

III. *Callorhynchus antarcticus* La C.; Cuv. Fig. 1, side, and 2, back, full length; 3, lower view of head.

IV. *Callorhynchus antarcticus.* Fig. 1, side, 2, top, and 3, lower view of head.

V. *Scoliodon terræ novæ* Rich.; Gill. Fig. 1, side, full length; 2, half of lower, 3, half of upper, and 4, front view of head.

VI. *Prionodon milberti* (Val.) M. & H. Fig. 1, side, full length; 2, lower, 3, front, and 4, upper view of head.

VII. *Cestracion tiburo* L.; Dum. (*Zygæna* auct.) Fig. 1, lower, and 2, upper view of head.

VIII. *Mustelus canis* Mitch.; DeKay. Fig. 1, side, entire; 2, lower, 3, front, and 4, top view of head.

IX. *Triacis semifasciatum* Girard. Fig. 1, side, entire; 2, lower, 3, front, and 4, top view of head.

X. *Isurus punctatus* sp. DeKay. Fig. 1, side, entire; 2, lower, 3, front, and 4, top view of head.

XI. *Odontaspis americanus* Mitch.; Abb. Fig. 1, entire side; 2, top, 3, front, and 4, lower view of head.

XII. *Alopias vulpes* Gmel.; Bonap. Fig. 1, front, 2, top, and 3, lower view of head.

XIII. *Alopias vulpes.* Entire view of side.

XIV. *Heptabranchias maculatus* Girard. Fig. 1, side, and 2, top view of head.

XV. *Chlamydoselachus anguineus* Garman. Fig. 1, side, and 2, top view of head.

XVI. *Ginglymostoma cirratum* Gmel.; M. & H. Fig. 1, entire side; 2, lower, 3, front, and 4, top view of head.

XVII. *Scyliorhinus caniculus* sp. Linn. Fig. 1, entire side; 2, lower, 3, front, and 4, top view of head.

XVIII. *Heterodontus philippi* La C.; Blainv. Fig. 1, entire side; 2, lower, 3, front, and 4, top view of head.

XIX. *Acanthias americanus* Storer. Fig. 1, entire side; 2, half of lower, 3, half of upper, and 4, front view of head; 5, side of tail; 6, section of canal at side of tail.

XX. *Somniosus carcharias* Müller; Garm. Fig. 1, top, and 2, lower view of head.

XXI. *Rhina squatina* L.; Dum. Fig. 1, top of head, with tubules; 2, full length, main tubes; 3, front, and 4, lower view of head.

XXII. *Pristiophorus cirratus* Lath.; M. & H. Fig. 1, top, and 2, lower view of head.

XXIII. *Pristis pectinatus* Latham. Fig. 1, top, and 2, lower view of anterior half of total length.

XXIV. *Rhinobatus planiceps* Garman. Fig. 1, top, and 2, lower view.

XXV. *Syrrhina brevirostris* Müller & Henle. Fig. 1, top, and 2, lower view.

XXVI. *Uraptera agassizii* M. & H. Fig. 1, lower, and 2, upper view.

XXVII. *Raia lævis* Mitchill. Upper surface, showing tubes and tubules.

XXVIII. *Raia lævis.* Upper view, showing (1) the hyaline mucous ducts of the "ampullæ of Lorenzini," and (2) the main tubes of the canal system.

XXIX. *Raia lævis.* Fig. 1, lower, and 2, upper view of head.

XXX. *Raia ocellata* Mitch. Fig. 1, top, and 2, lower view of disk.

XXXI. *Torpedo californica* Ayres. Upper view.

XXXII. *Torpedo marmorata* Risso. Upper view.

XXXIII. *Narcine brasiliensis* Oif.; Henle. Upper view.

XXXIV. *Potamotrygon motoro* M. & H.; Garm. Fig. 1, upper, 2, lower surface.

XXXV. *Disceus strongylopterus* Schomb.; Garm. Fig. 1, upper, 2, lower surface.

XXXVI. *Urolophus halleri* Cooper. Upper view.

XXXVII. *Urolophus halleri.* Lower view.

XXXVIII. *Tæniura lymma* Cuv.; M. & H. Fig. 1, upper, and 2, lower view.

XXXIX. *Dasybatus nudus* Gthr.; Garm. Fig. 1, upper, and 2, lower view.

XL. *Dasybatus dipterurus* Jordan. Fig. 1, lower, and 2, upper view.

XLI. *Dasybatus tuberculatus* La C.; Garm. Lower view.

XLII. *Dasybatus tuberculatus.* Upper view.

XLIII. Fig. 1. *Pteroplatea hirundo* Lowe. Upper view. Fig. 2. *Pteroplatea marmorata* Cooper. Upper view.

XLIV. *Pteroplatea valenciennii* Duméril. Upper surface.

XLV. *Pteroplatea valenciennii.* Fig. 1, upper, and 2, lower view.

XLVI. *Myliobatis aquila* L.; Cuv. Upper surface.

XLVII. *Myliobatis aquila.* Fig. 1, lower surface, and 2, side of head.

XLVIII. *Myliobatis freminvillii* Lesueur. Fig. 1, upper, and 2, lower view.

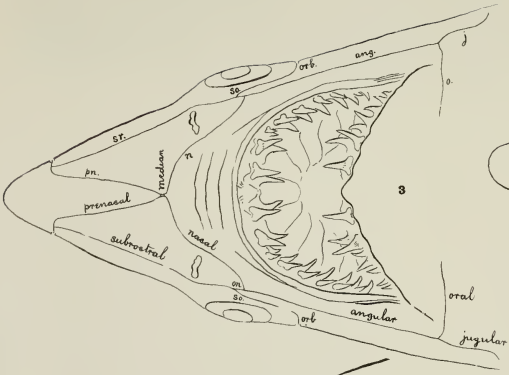
XLIX. *Aëtobatis narinari* Euph.; M. & H. Fig. 1, upper, and 2, lower surface; 3, lower view of end of pectoral; 4, side and lower view of head; 5, tail and hinder part of body.

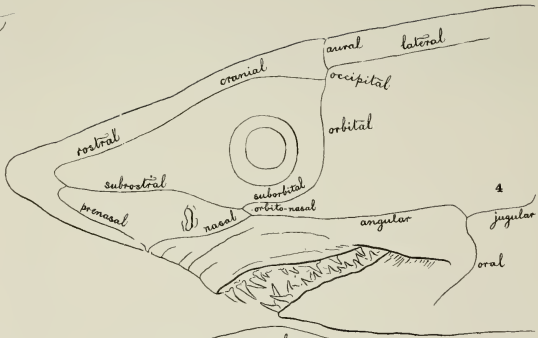
L. *Rhinoptera brasiliensis* Müller. Fig. 1, upper, and 2, lower view of disk; 3, lower side of end of pectoral fin; 4, side and lower view of head.

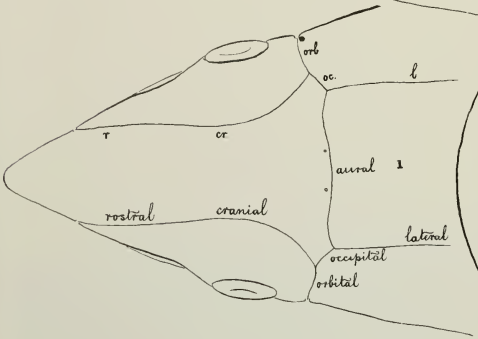
LI. *Rhinoptera jussieui* Cuv.; Gthr. Fig. 1, upper, 2, lower, and 3, side and lower view of head.

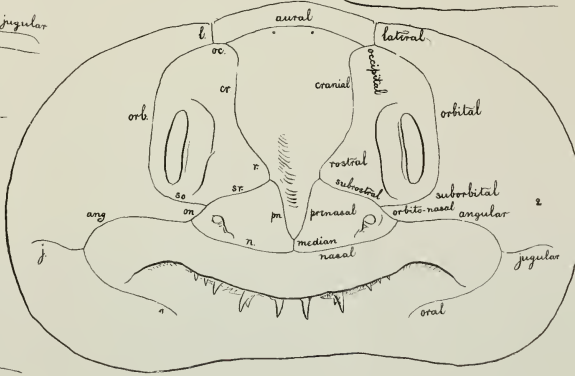
LII. *Dicerobatus olfersii* Müller; Gthr. Fig. 1, upper surface; 2, side of head.

LIII. *Dicerobatus olfersii.* Lower surface.









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ISURUS PUNCTATUS.

CHIMAERA MONSTROSA.

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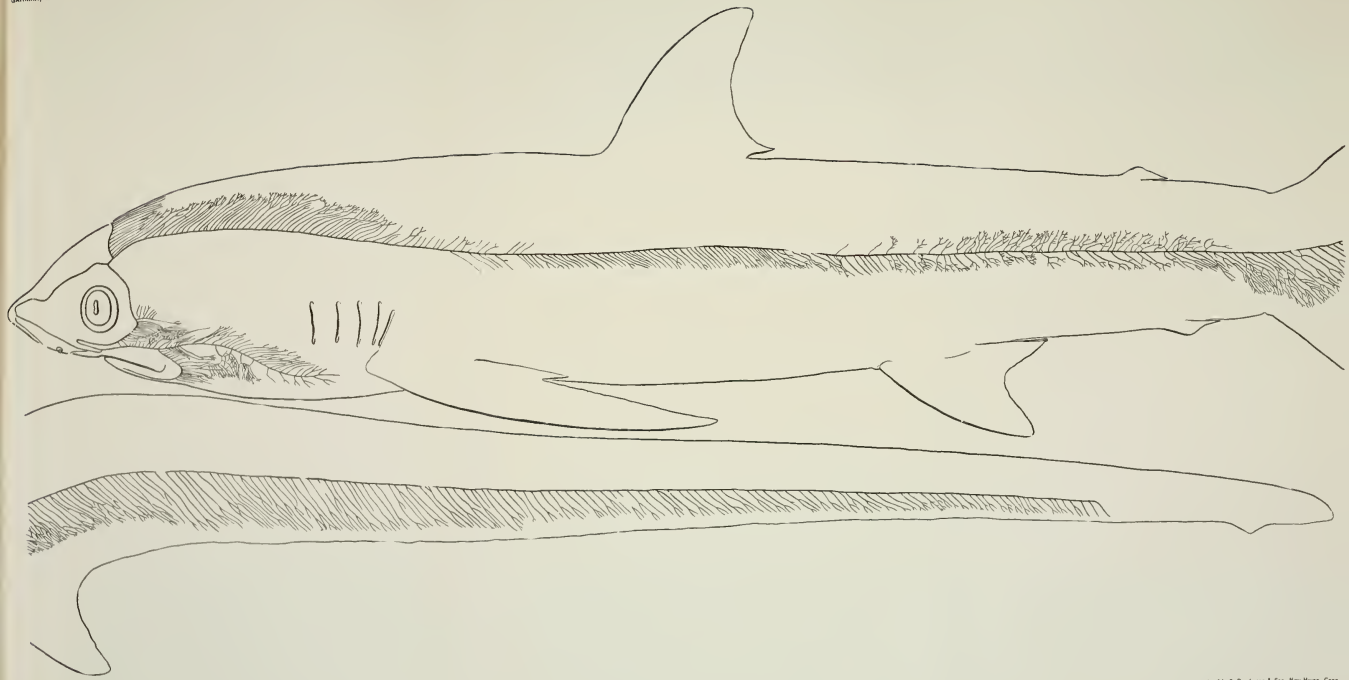

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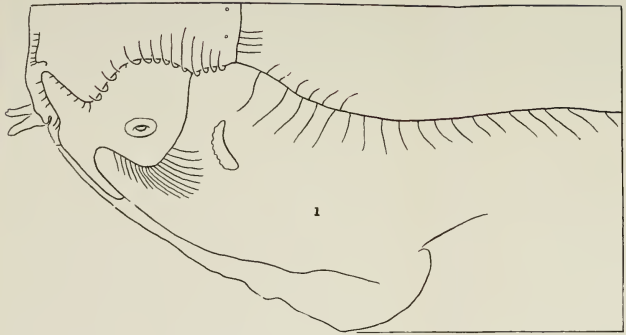

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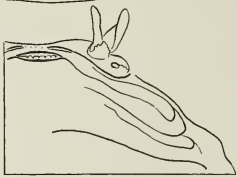

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RHINA SQUATINA.

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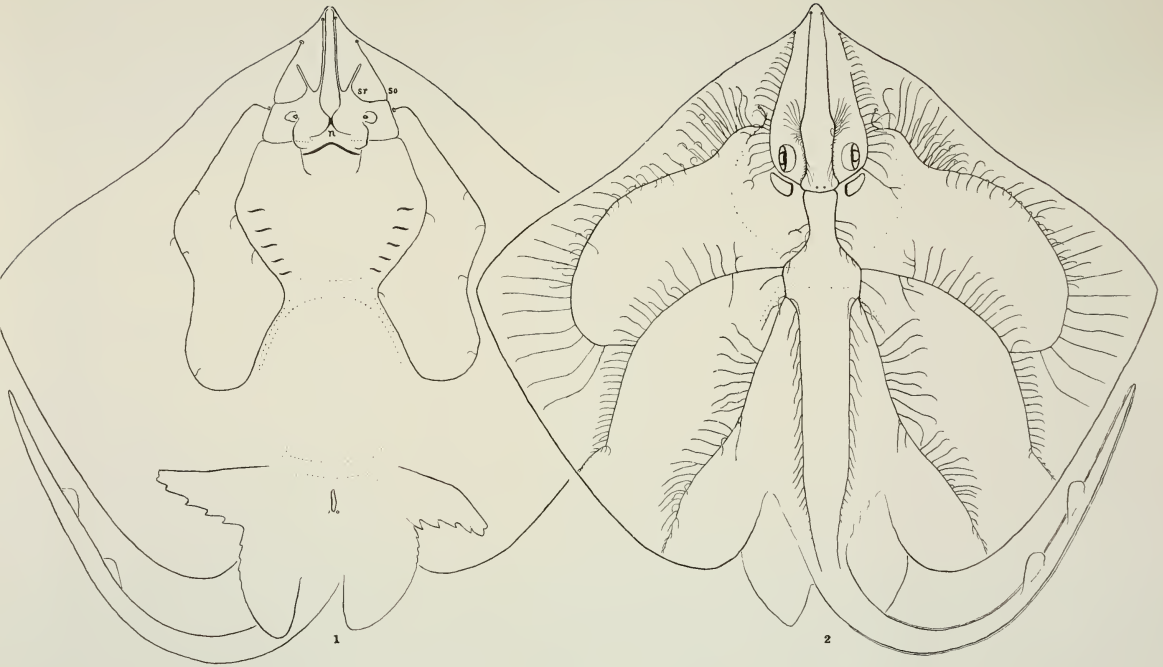

URAPTERA AGASSIZII.

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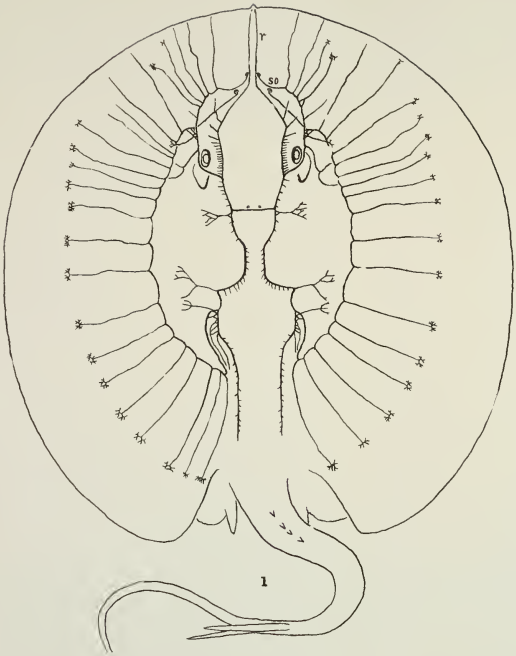

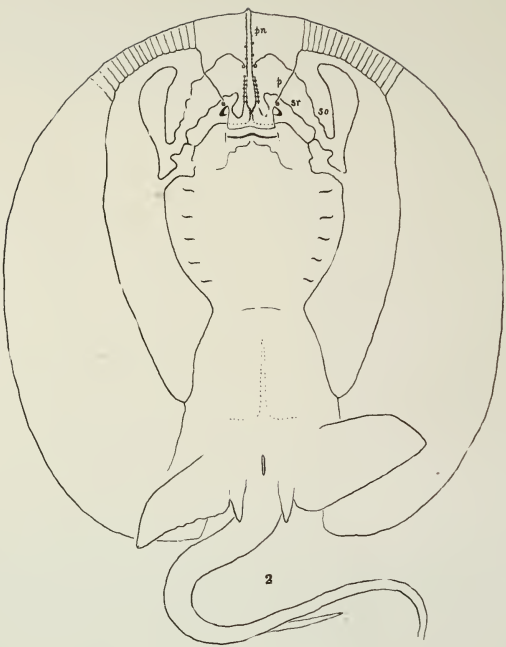

POTAMOTRYGON MOTORO.

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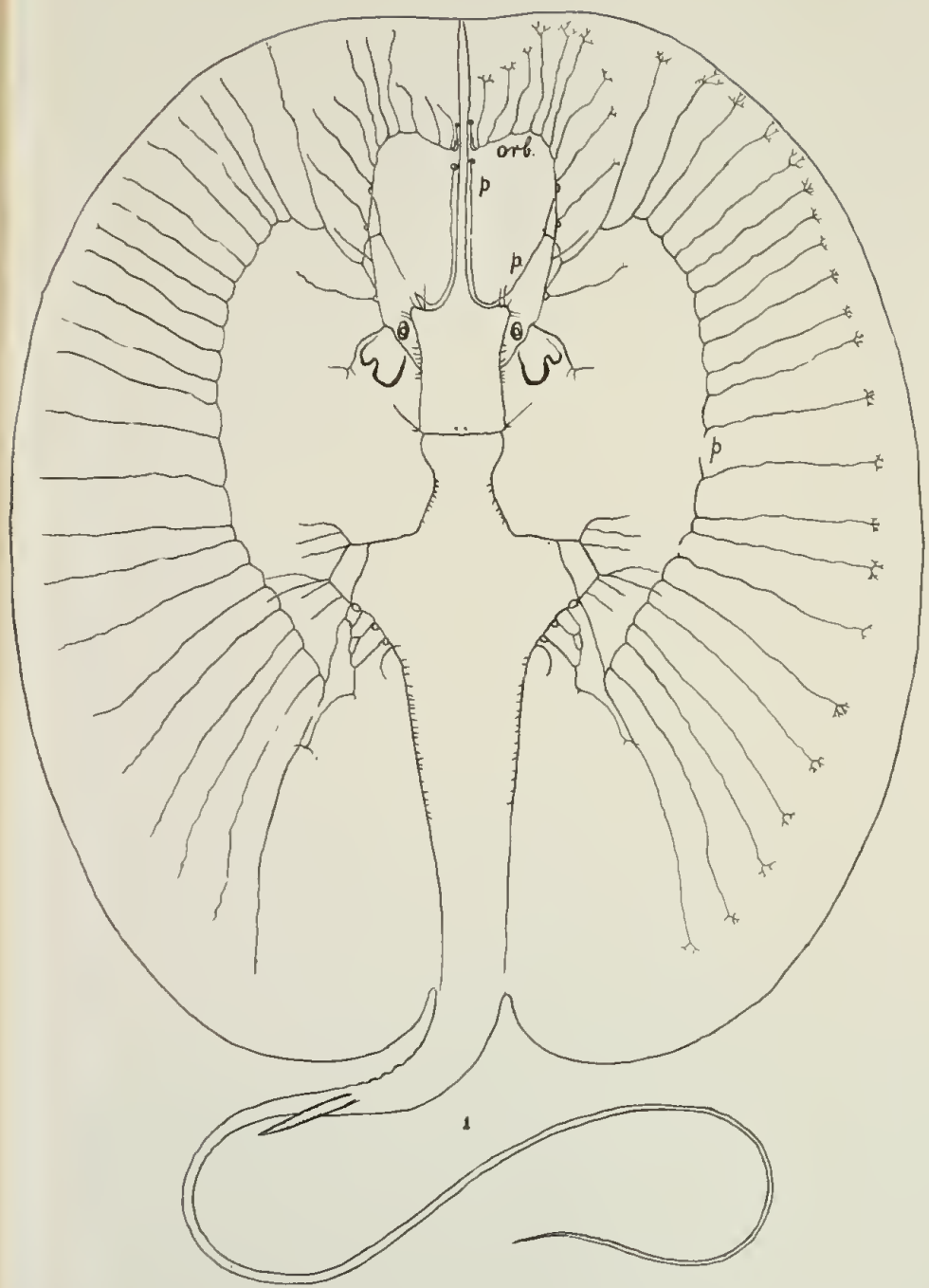

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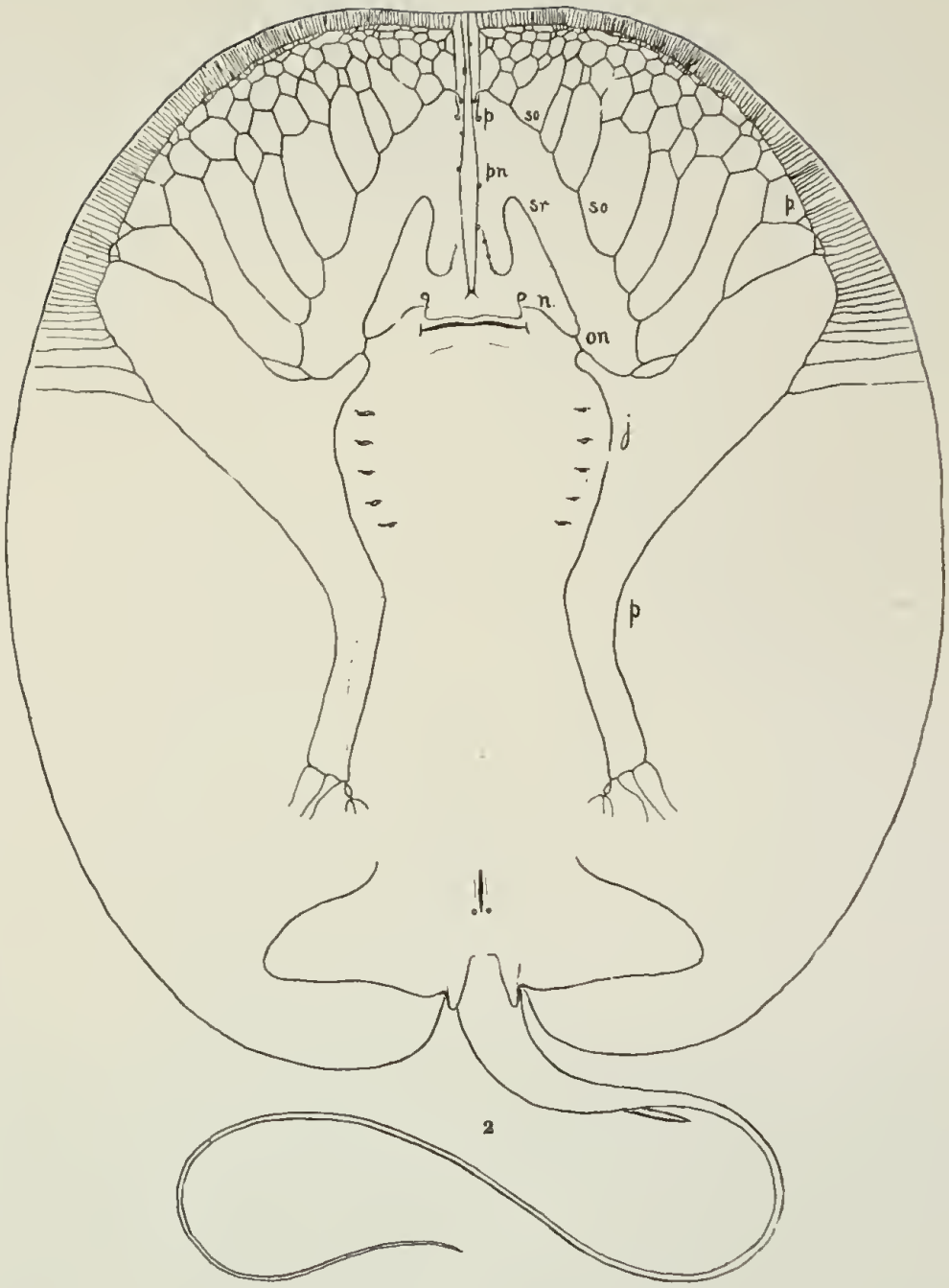

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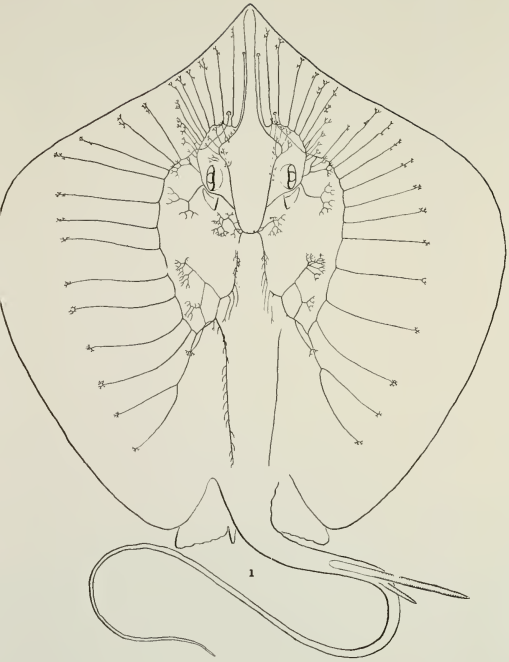
DISCEUS STRONGYLOPTERUS.



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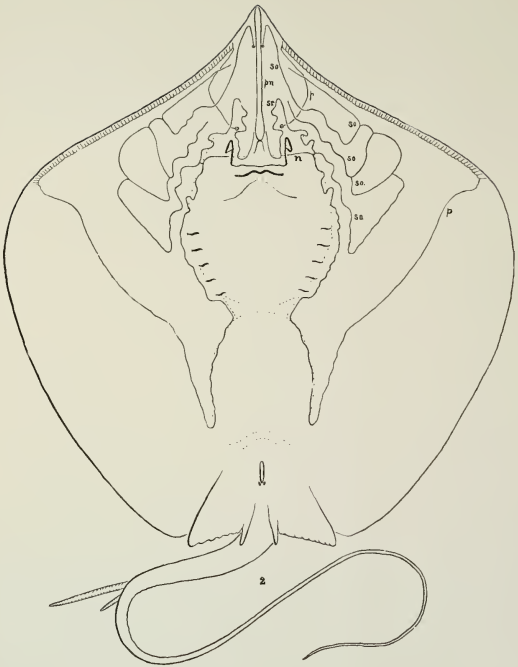

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DASYBATUS NUDUS.

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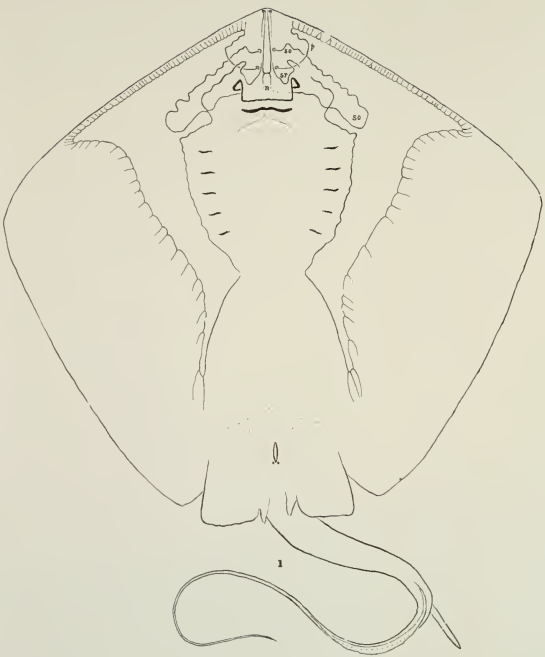

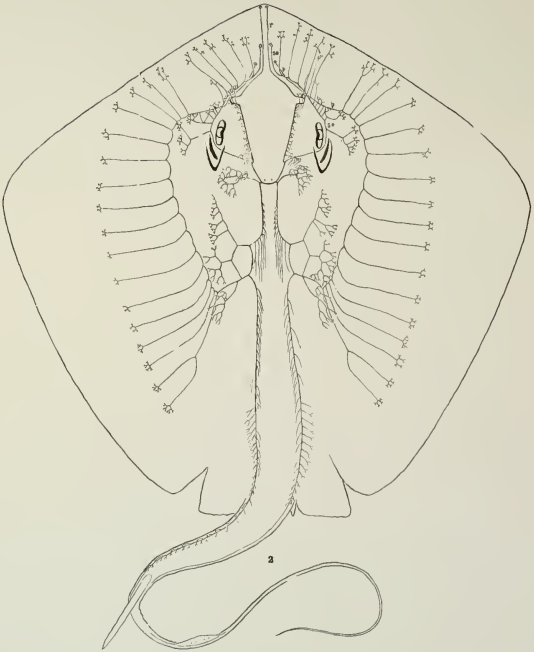

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DASYBATUS DIPTERURUS.

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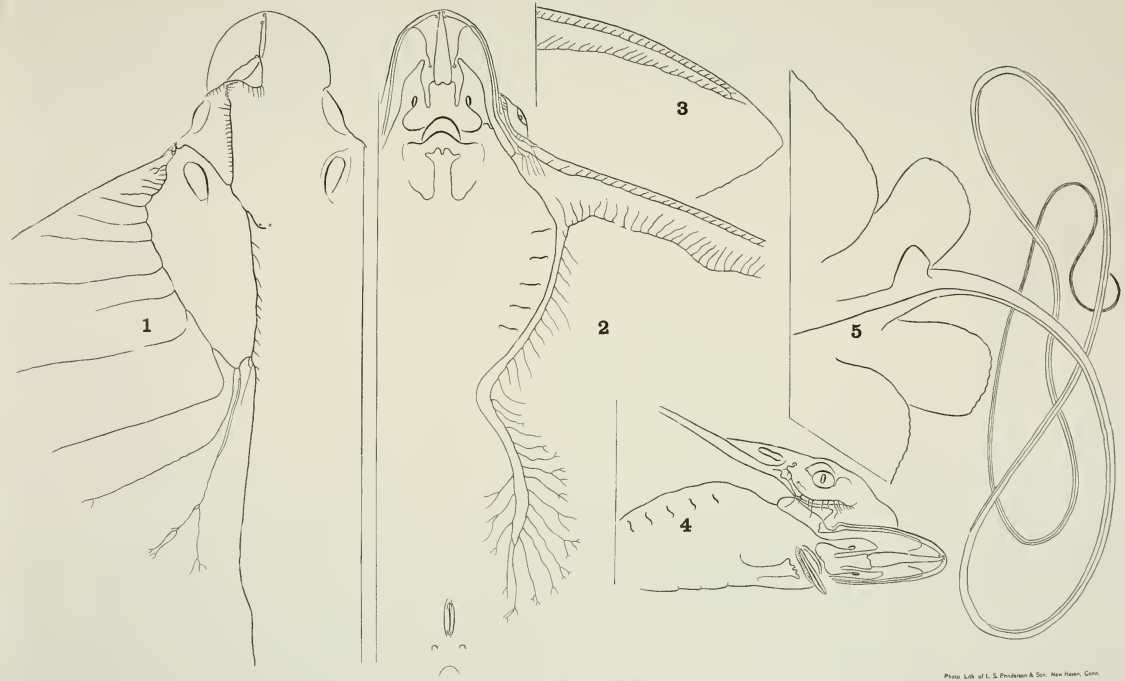

AETOBATUS NARINARI.

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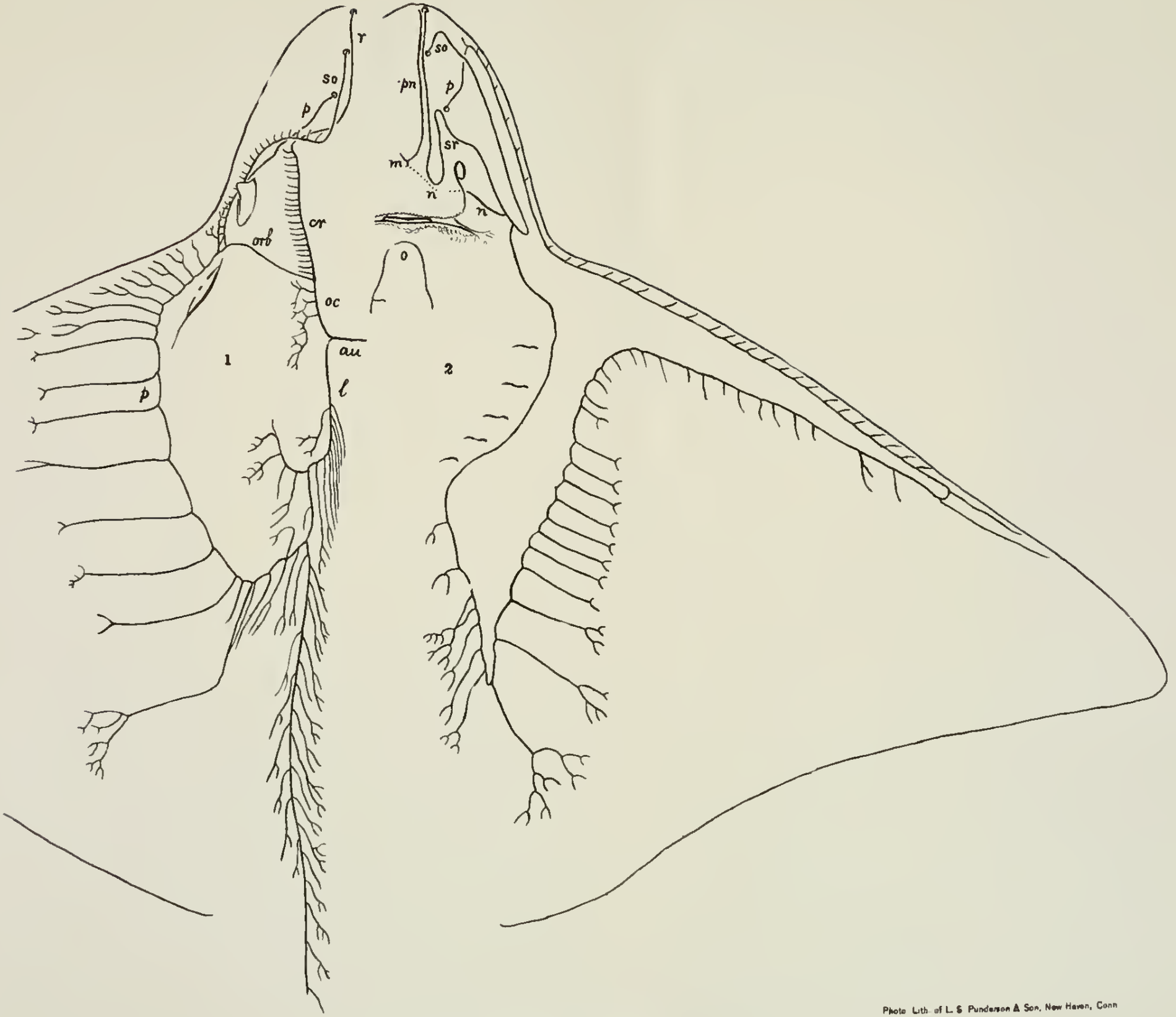

MYLIOBATIS FREMINVILLEI.

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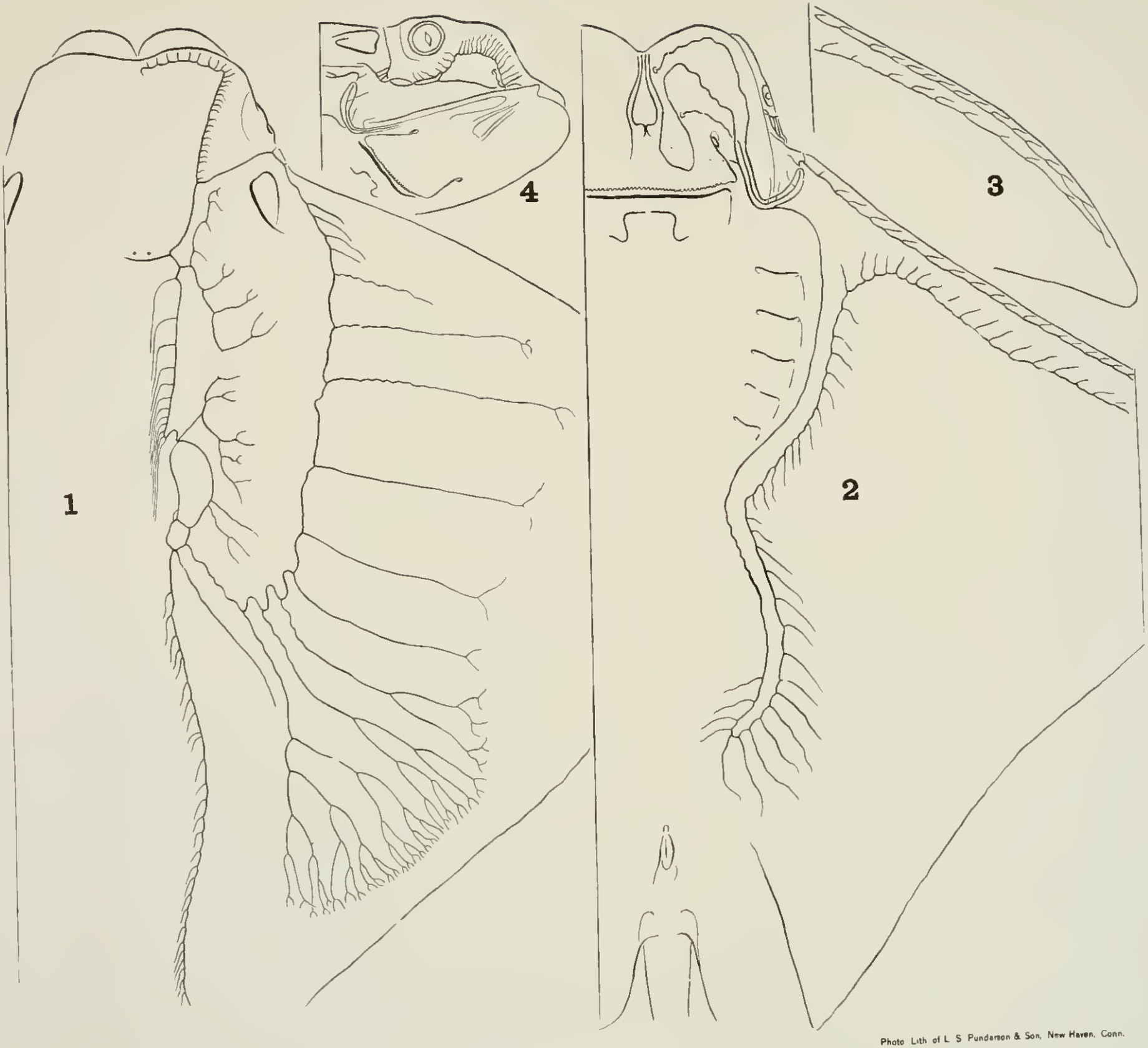

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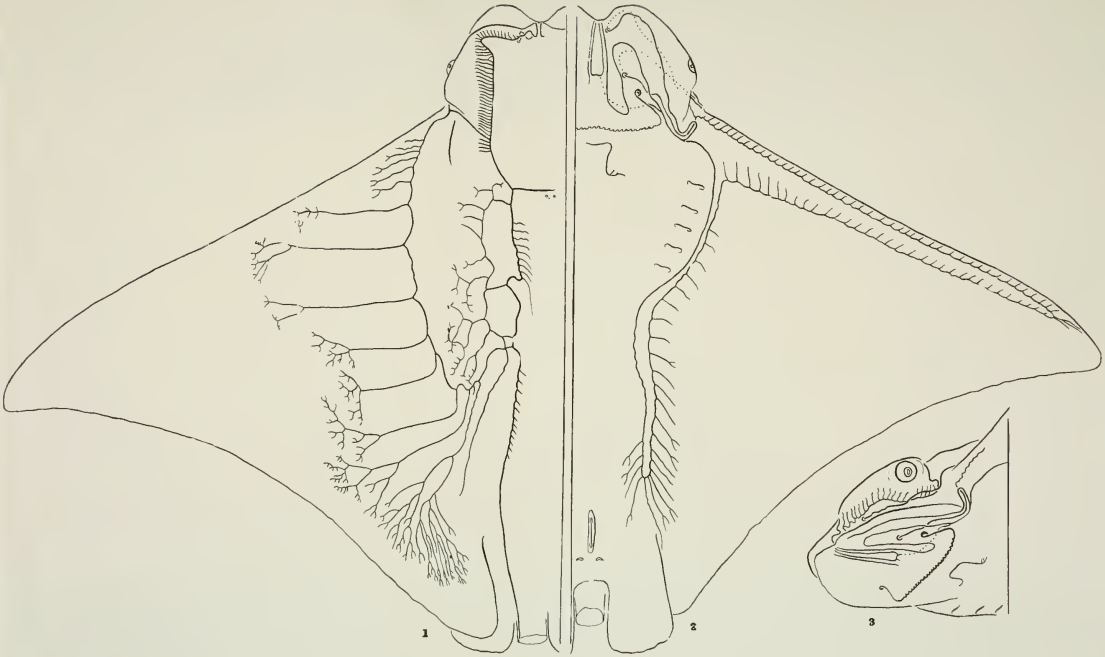
RHINOPTERA BRASILIENSIS.



RHINOPTERA JUSSIEUI.

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DICEROBATUS OLFERSII.

DICEROBATUS OLFERSII.

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CALLORHYNCHUS ANTARCTICUS.

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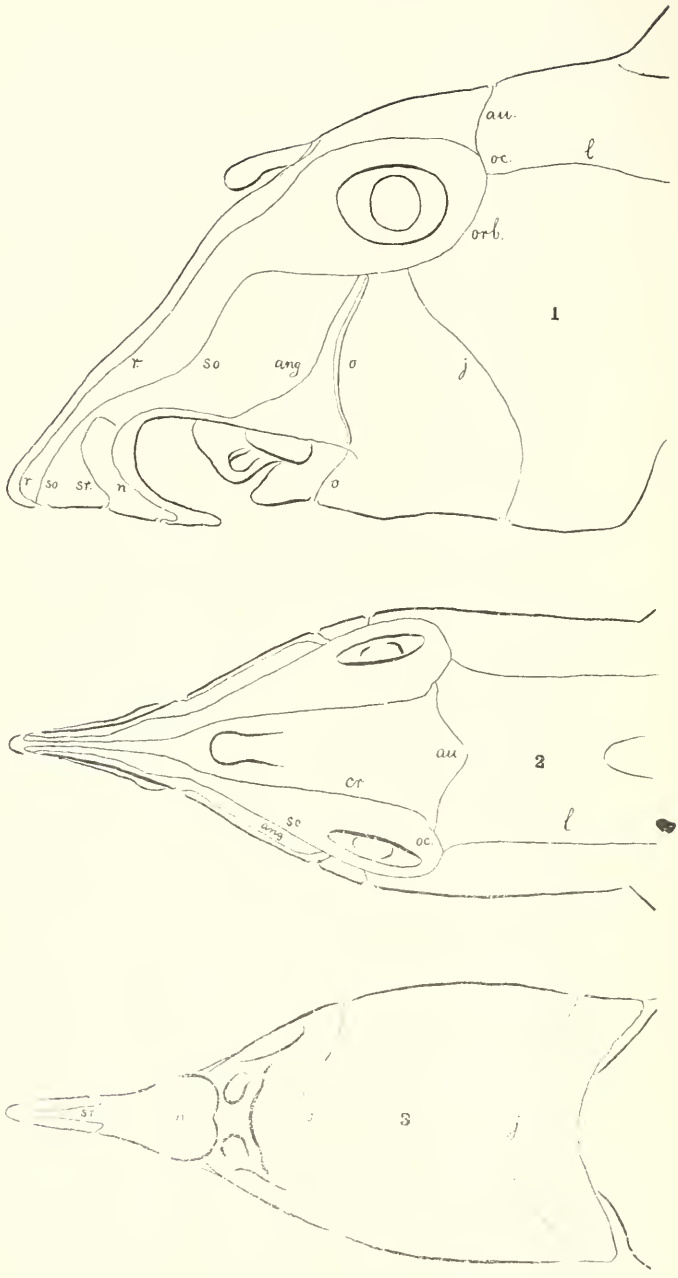

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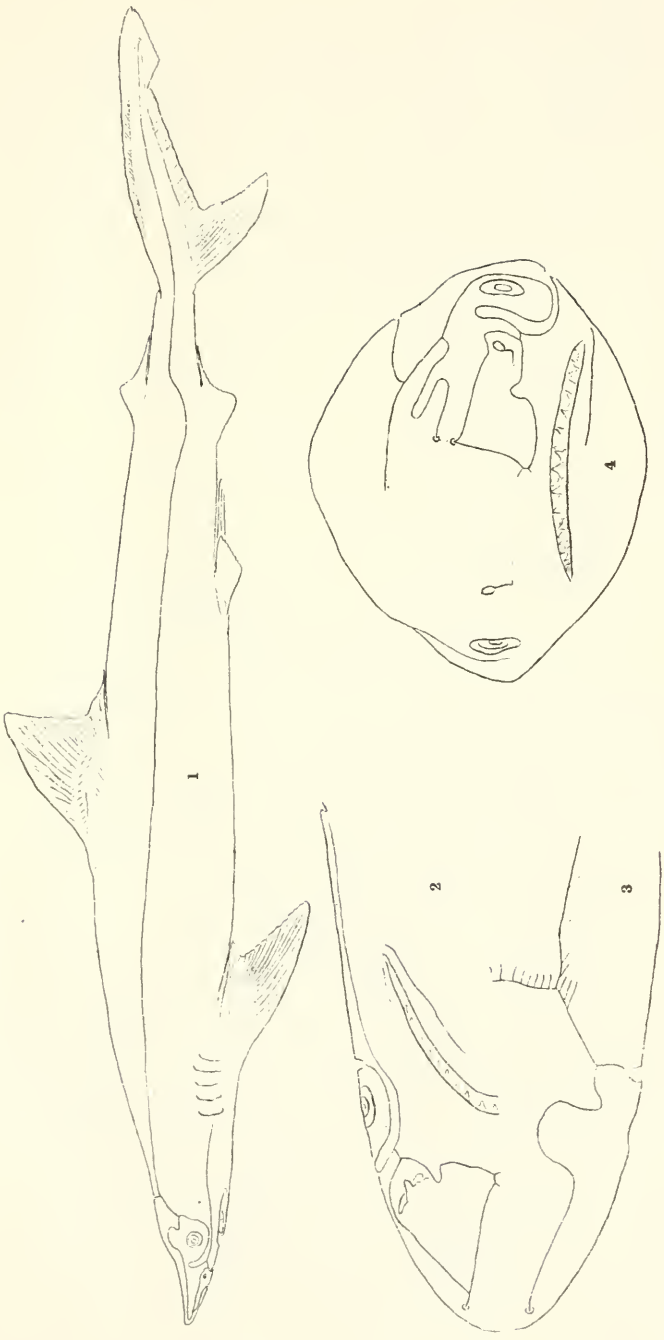
CALLORHYNCHUS ANTARCTICUS.



SCOLIODON TERRAE NOVAE.

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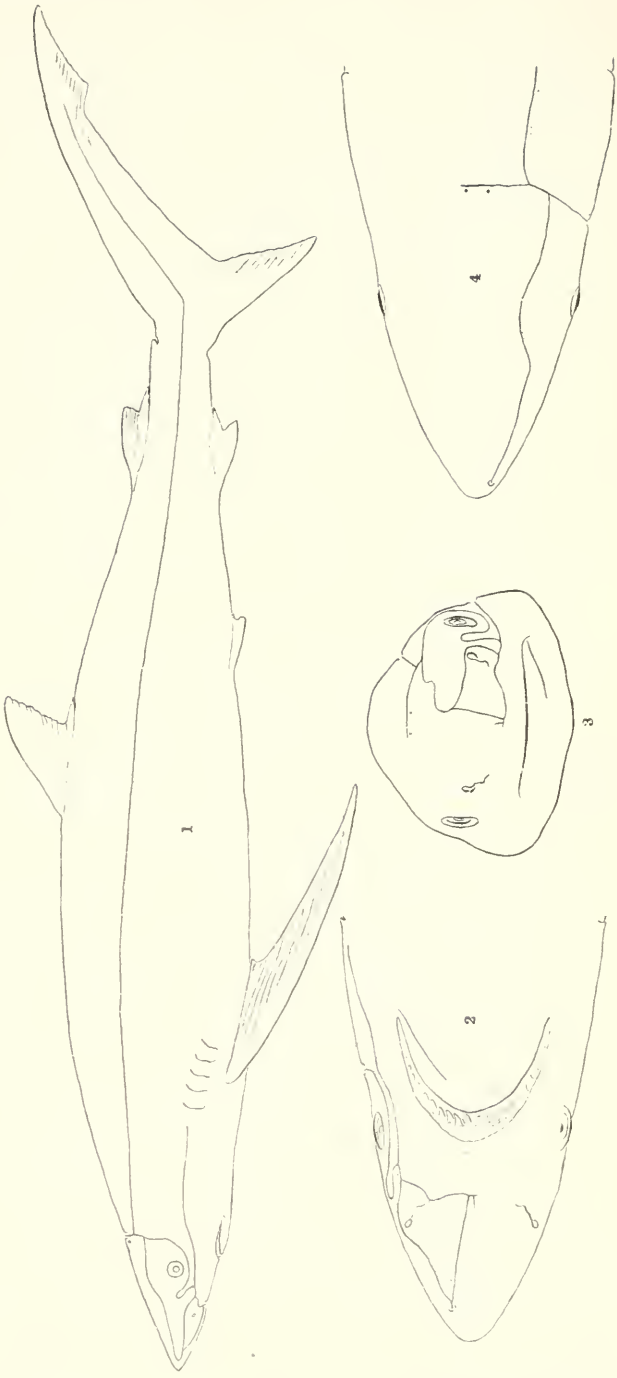

PRIO'ODON MILBERTI.

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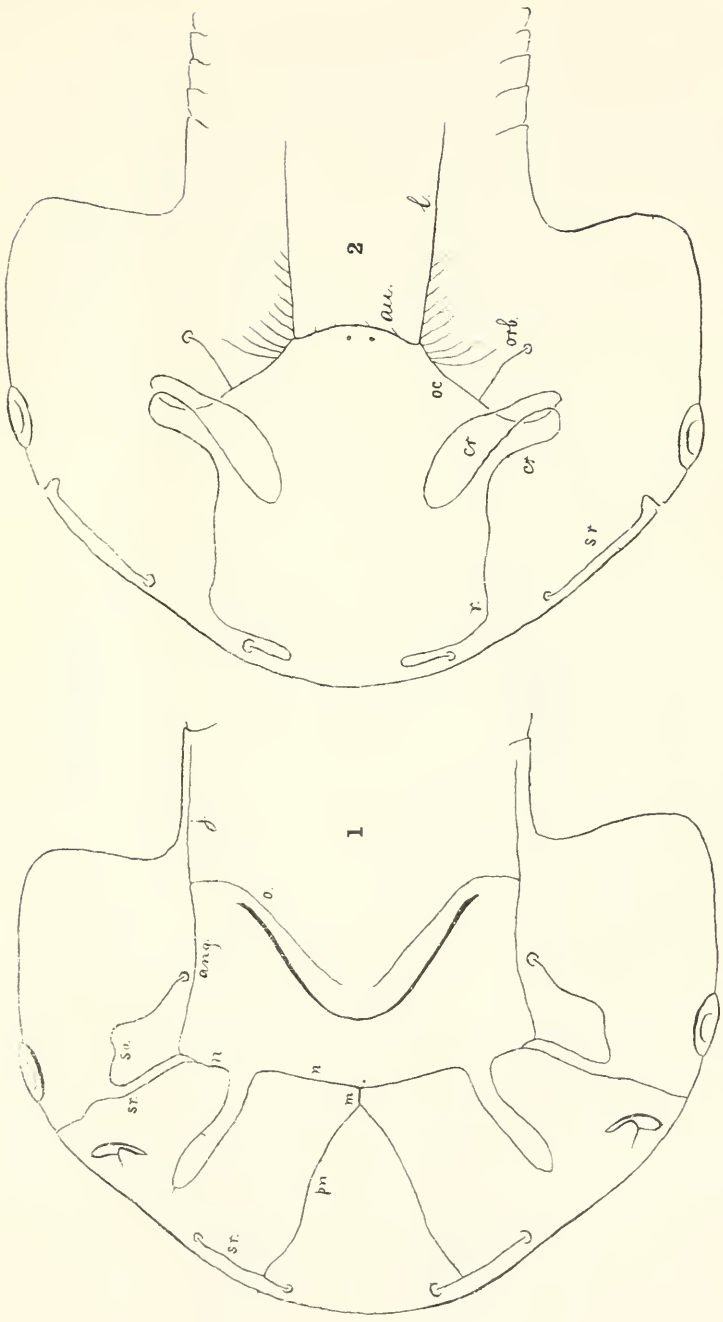

CESTRACION TIBURO.

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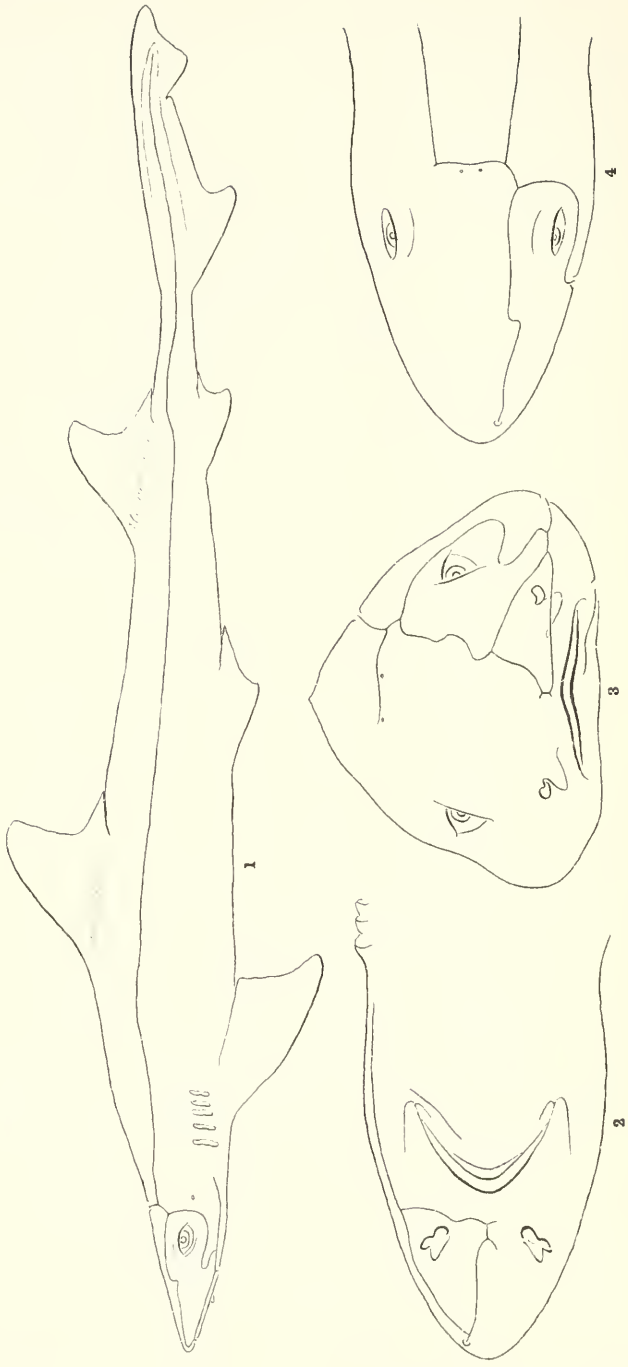

MUSTELUS CANIS.

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TRIACIS SEMIFASCIATUM.

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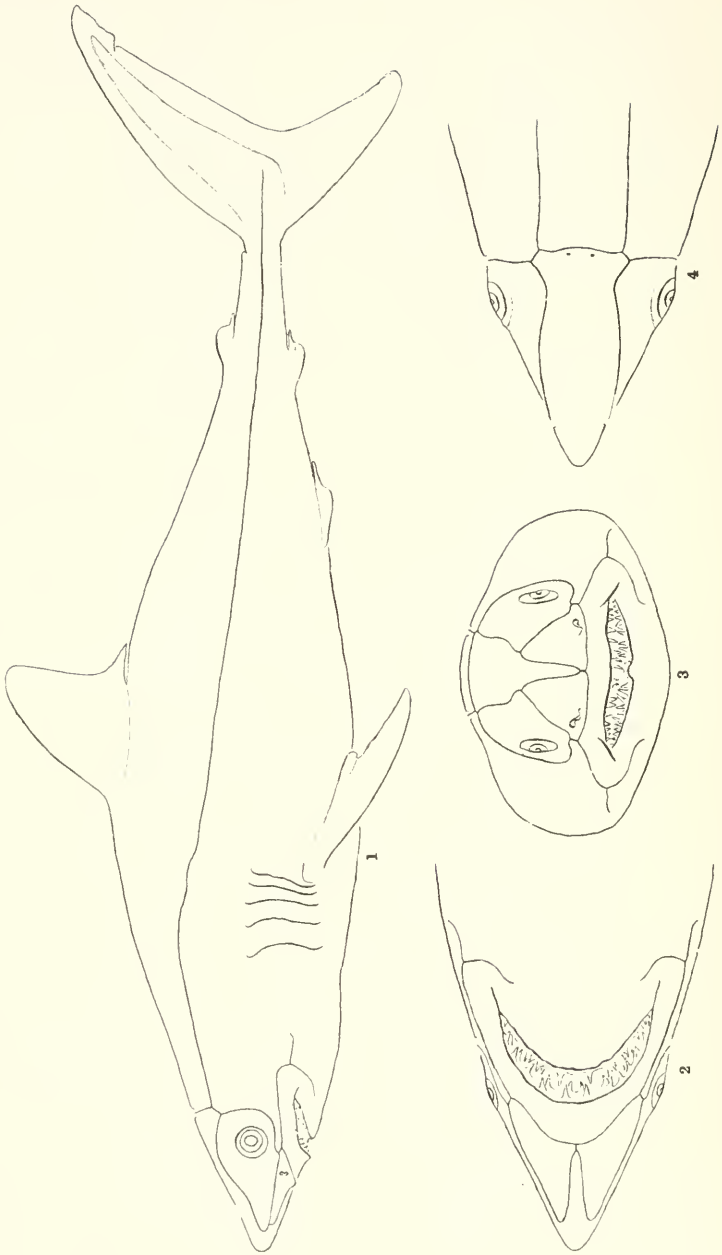

ISURUS PUNCTATUS.

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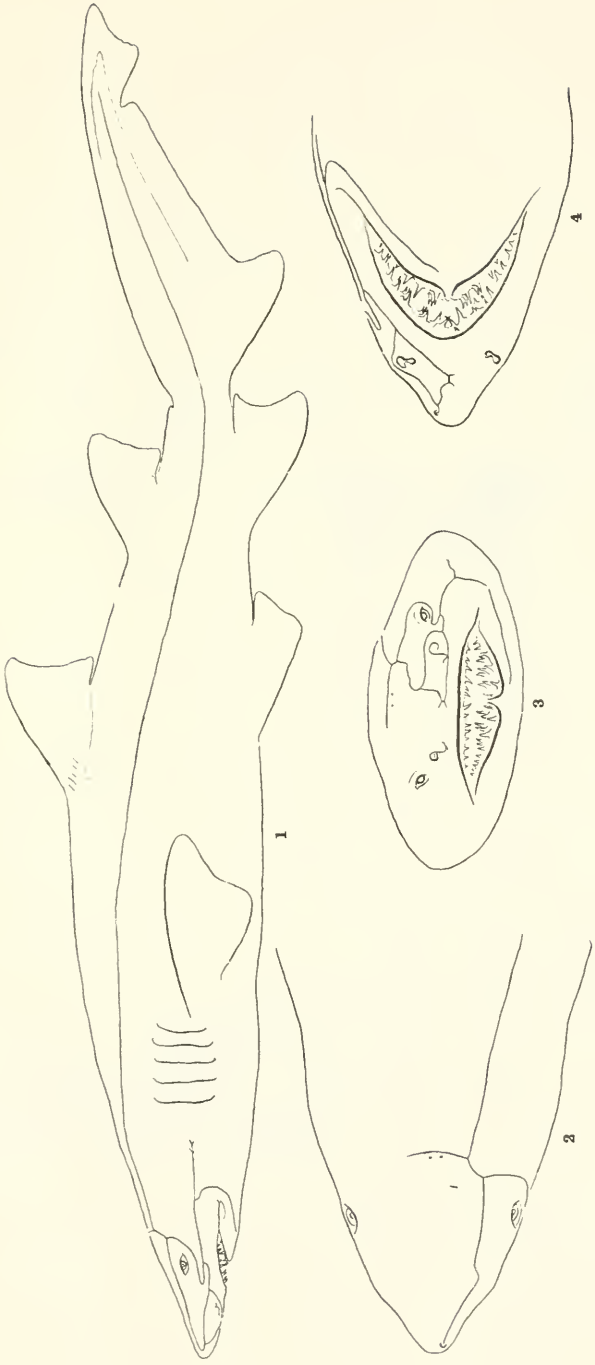

ODONTASPIS AMERICANUS

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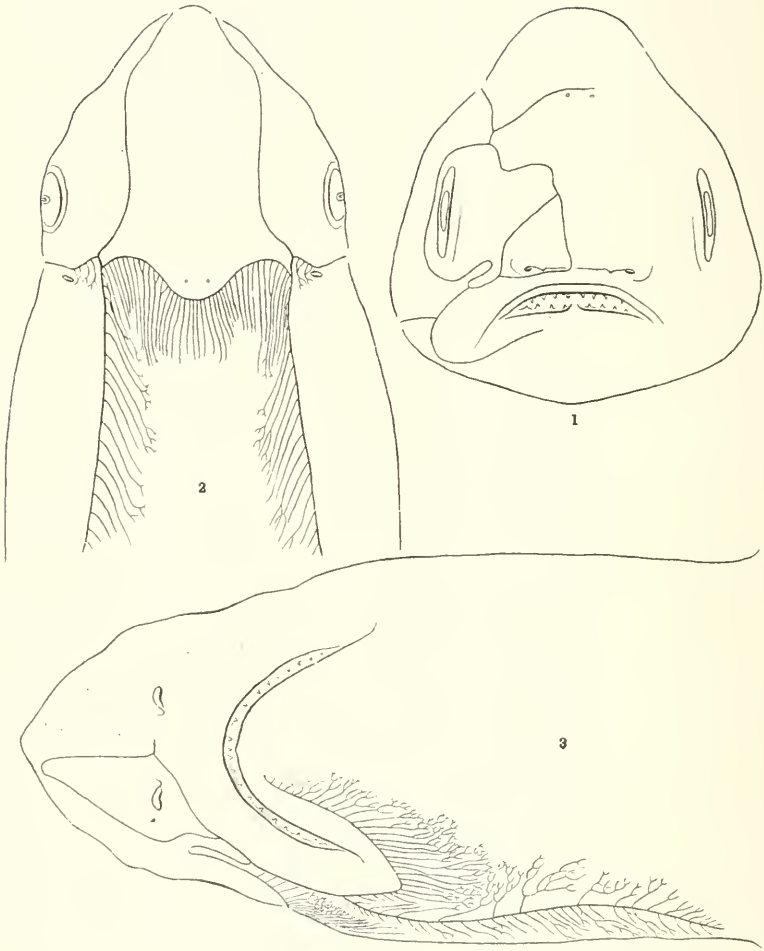

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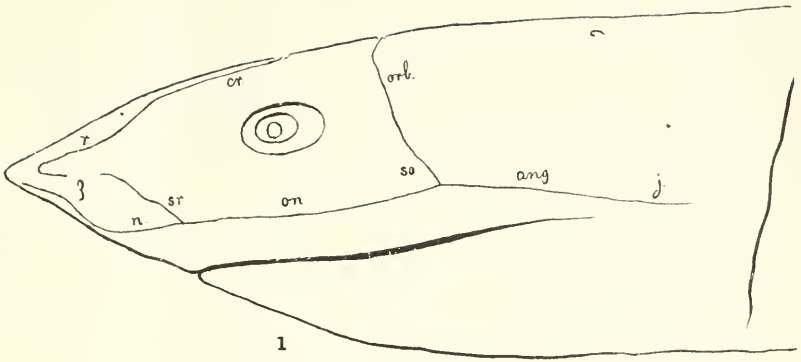
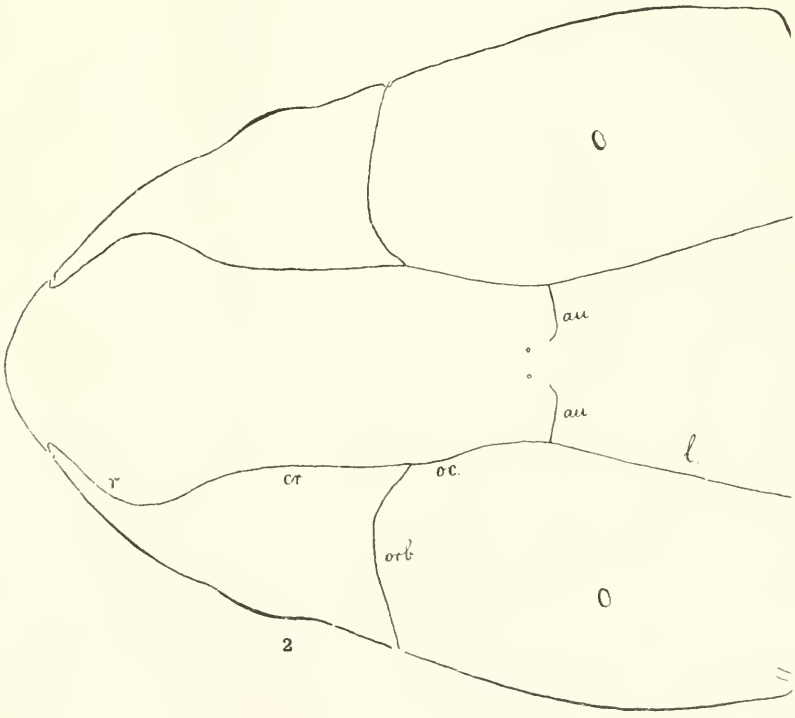
ALOPIAS VULPES.





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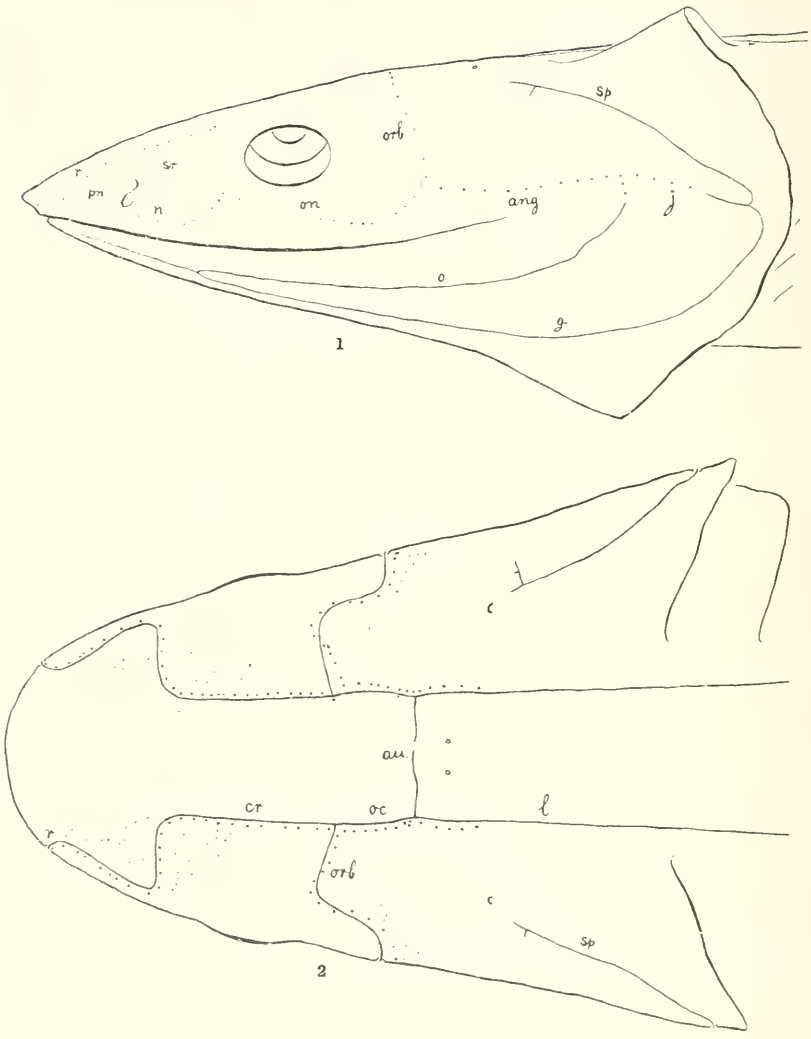
HEPTABRANCHIAS MACULATUS.



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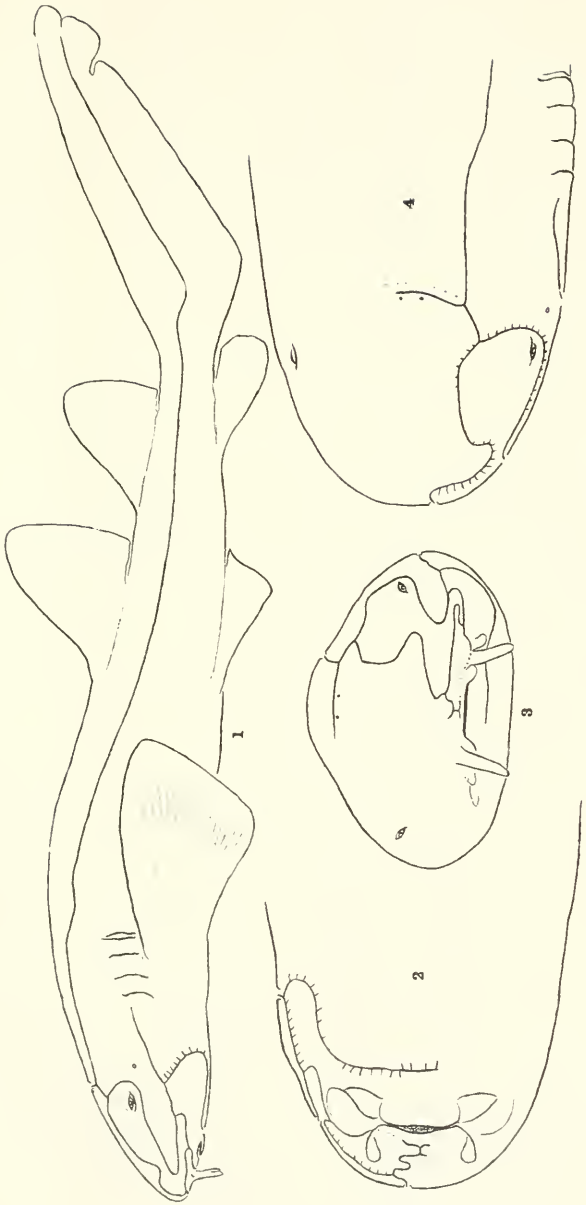
CHLAMYDOSELACHUS ANGUINEUS.



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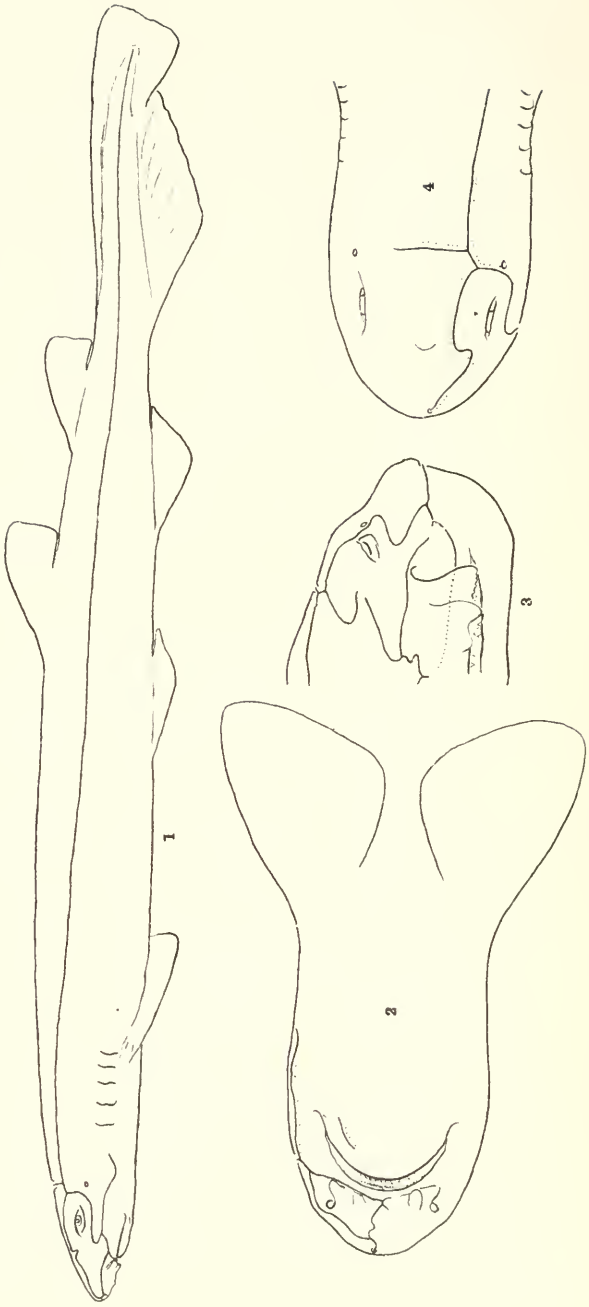

SCYLLIORHINUS CANICULUS.

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HETERODONTUS PHILIPPI.

Photo. Lith. of L. S. Punderson & Son, New Haven Conn.

ACANTHIAS AMERICANUS.

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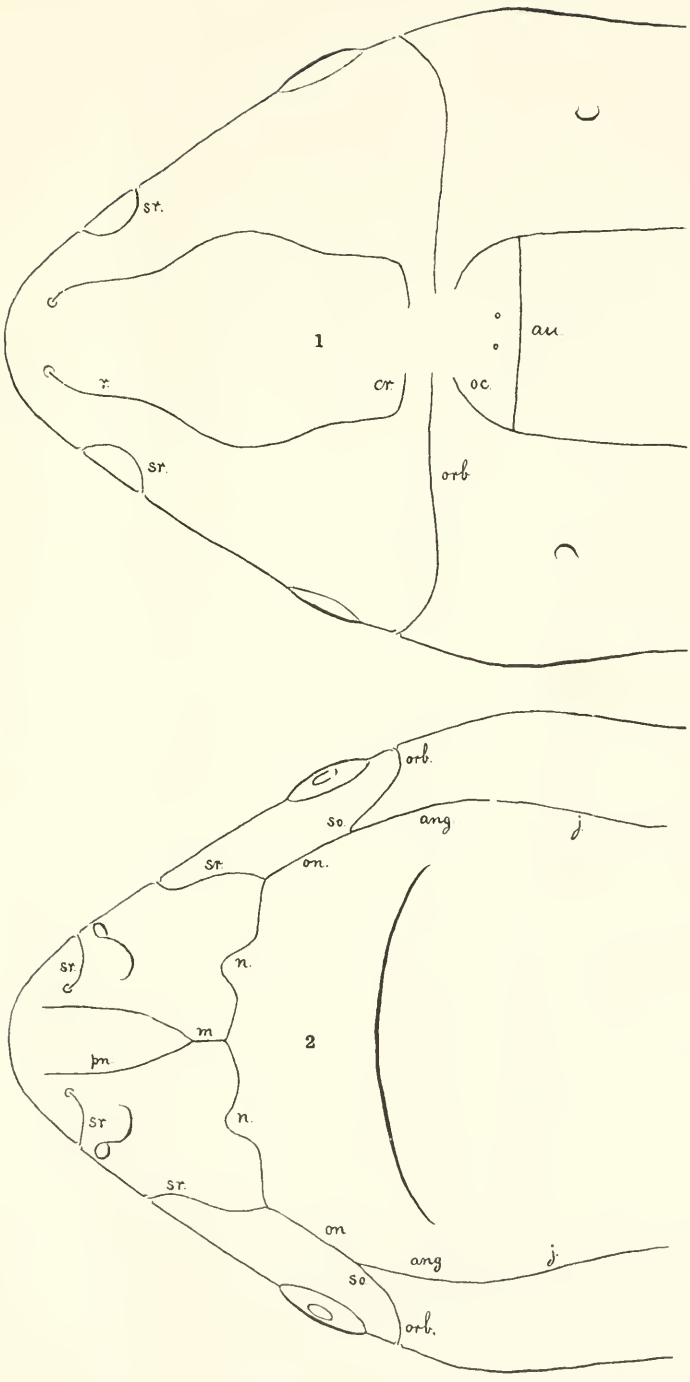

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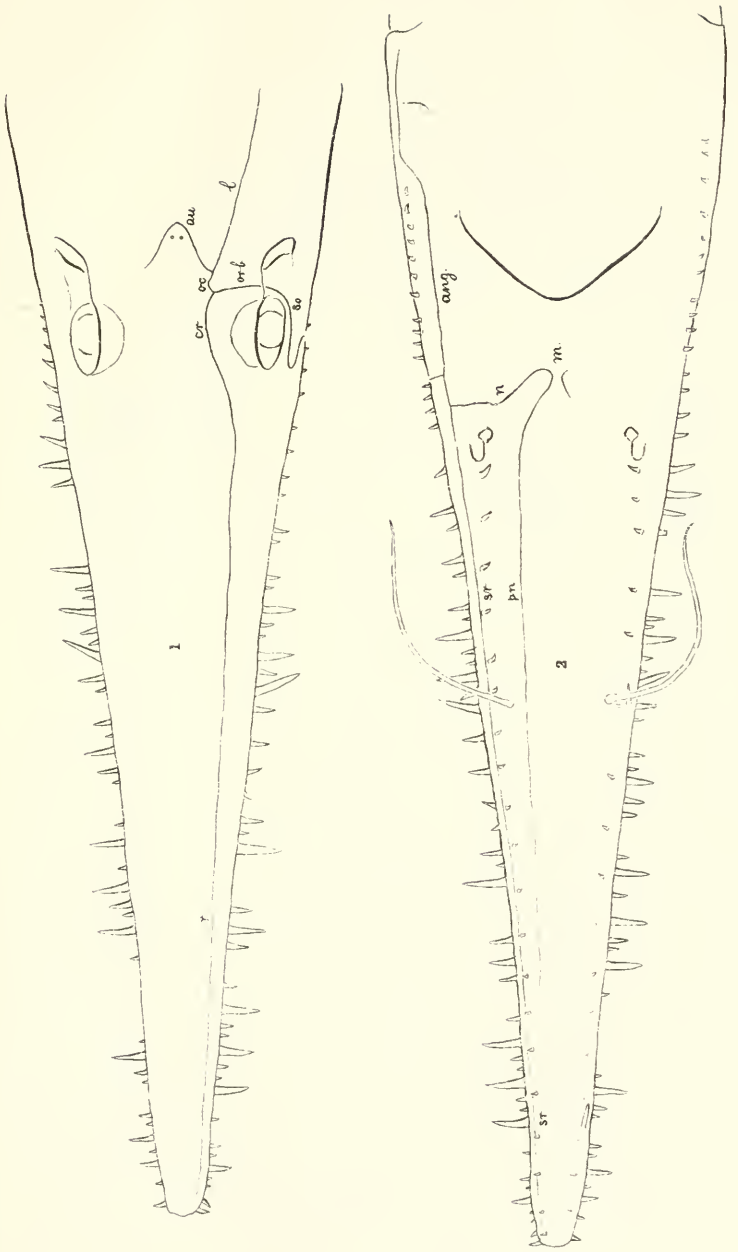
SOMNIOSUS CARCHARIAS.



PRISTIOPHORUS CIRRATUS.

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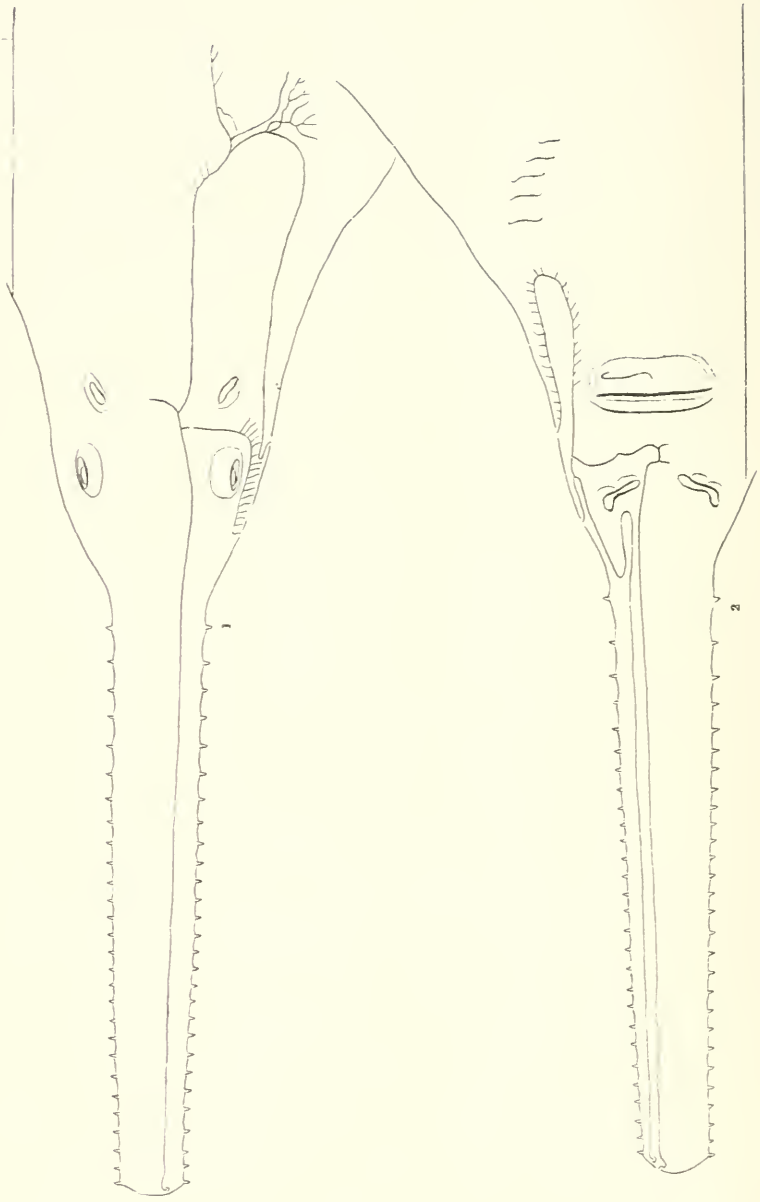

PRISTIS PECTINATUS.

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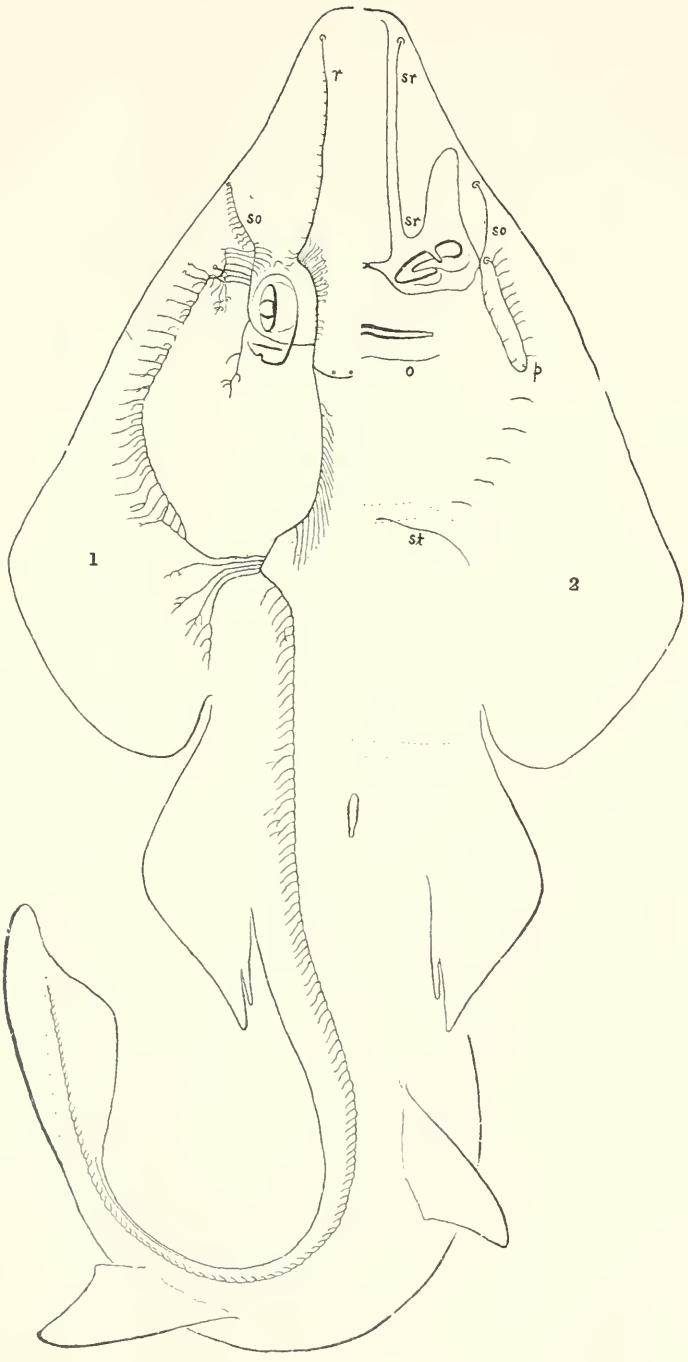

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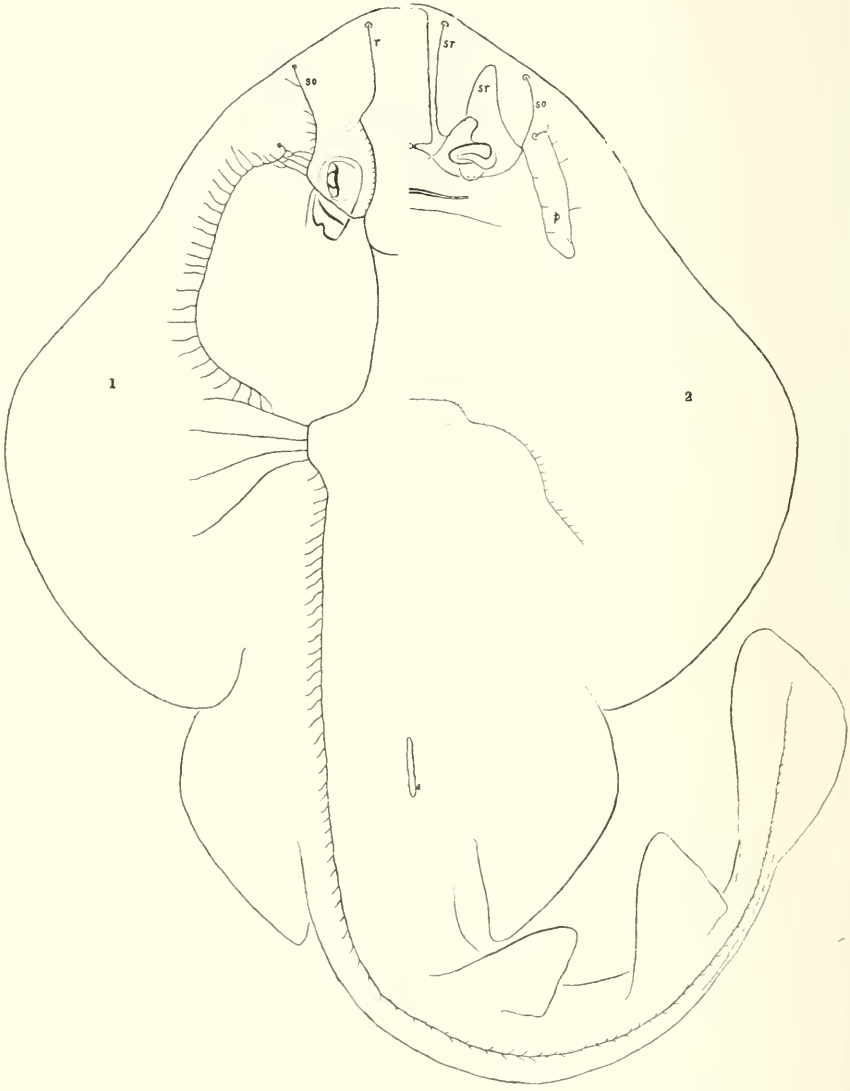
RHINOBATUS PLANICEPS.



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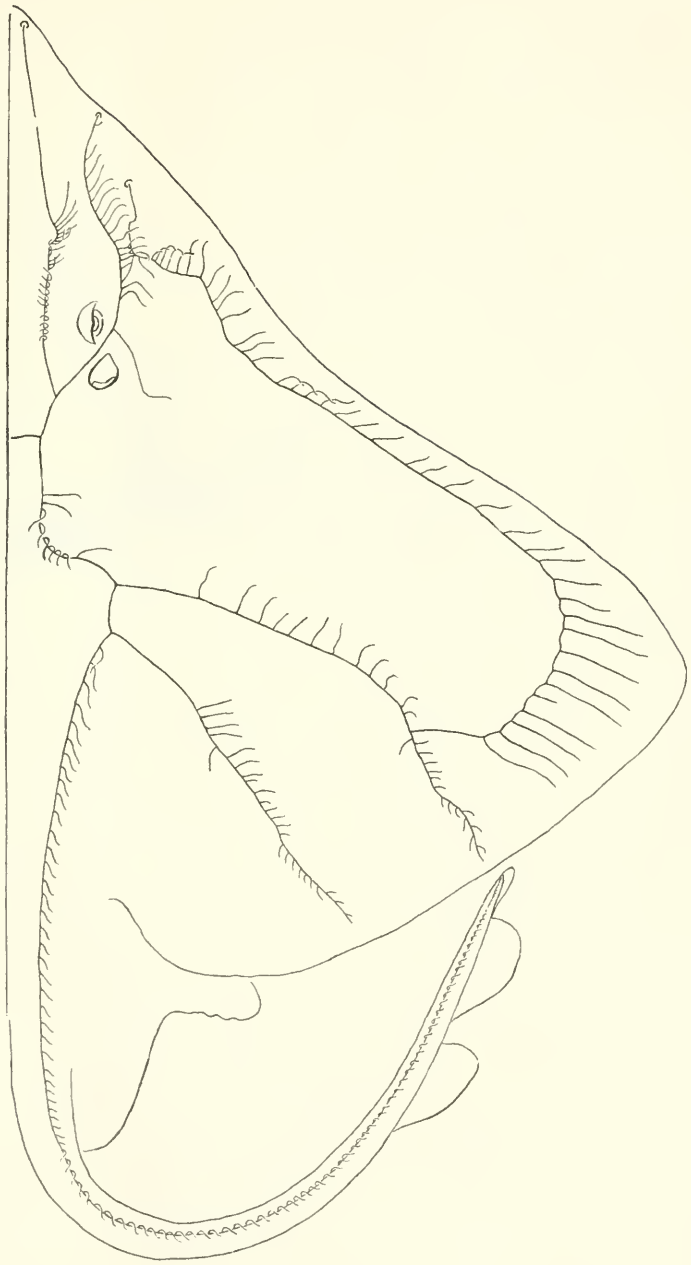
SYRRHINA BREVIROSTRIS.



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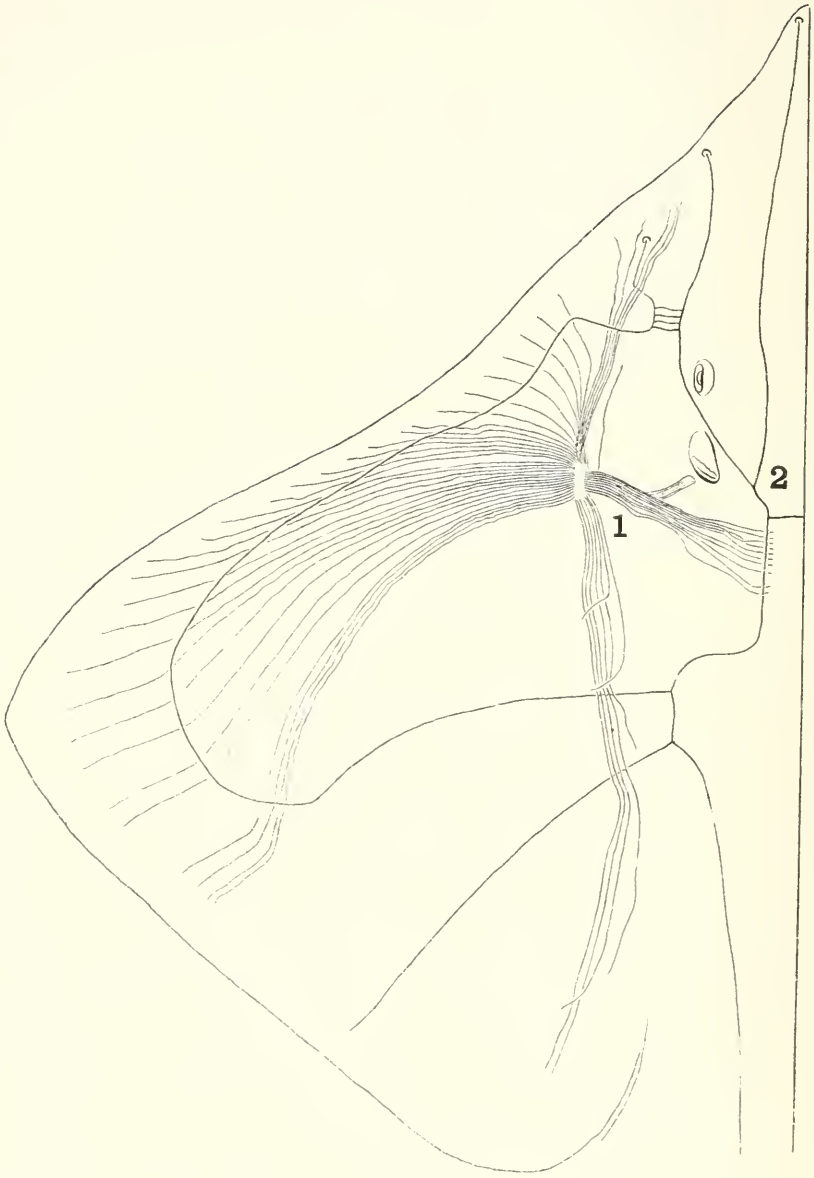
RAIA LAEVIS.



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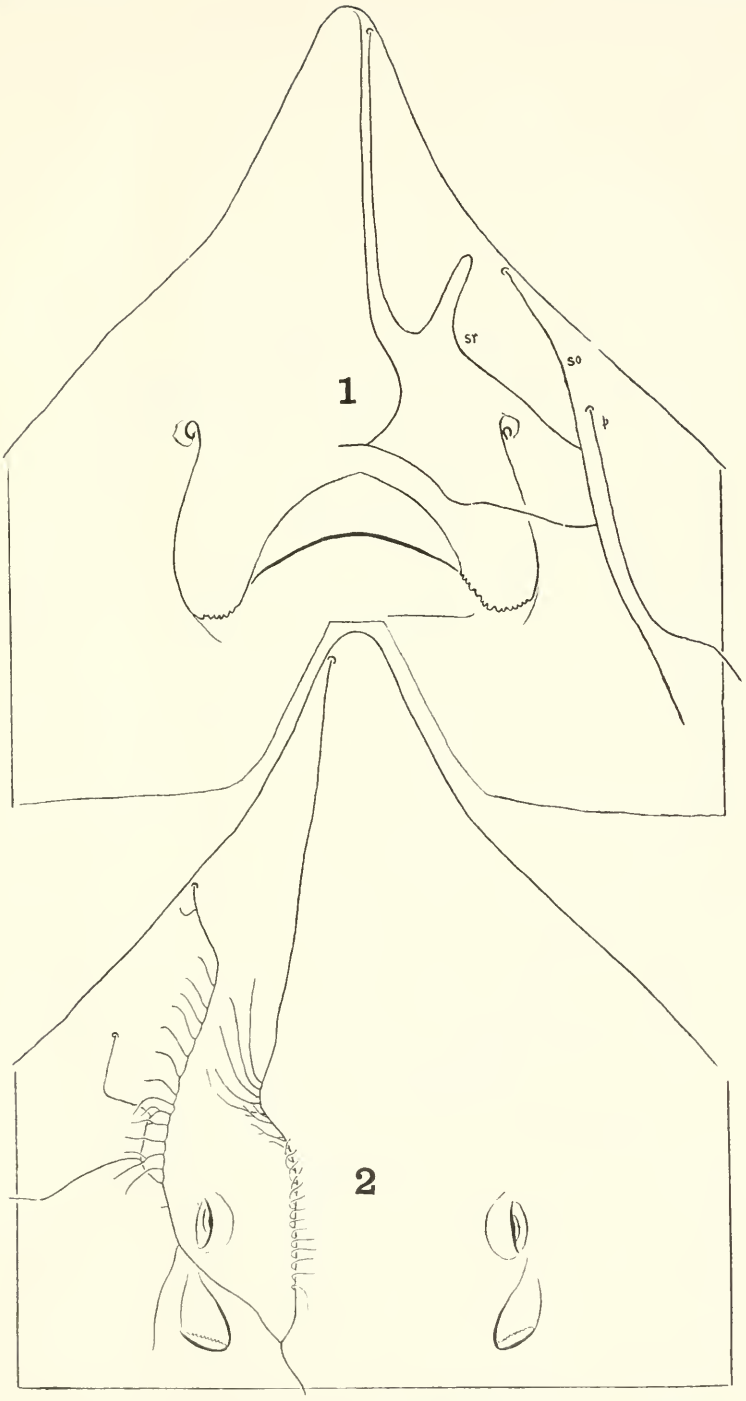

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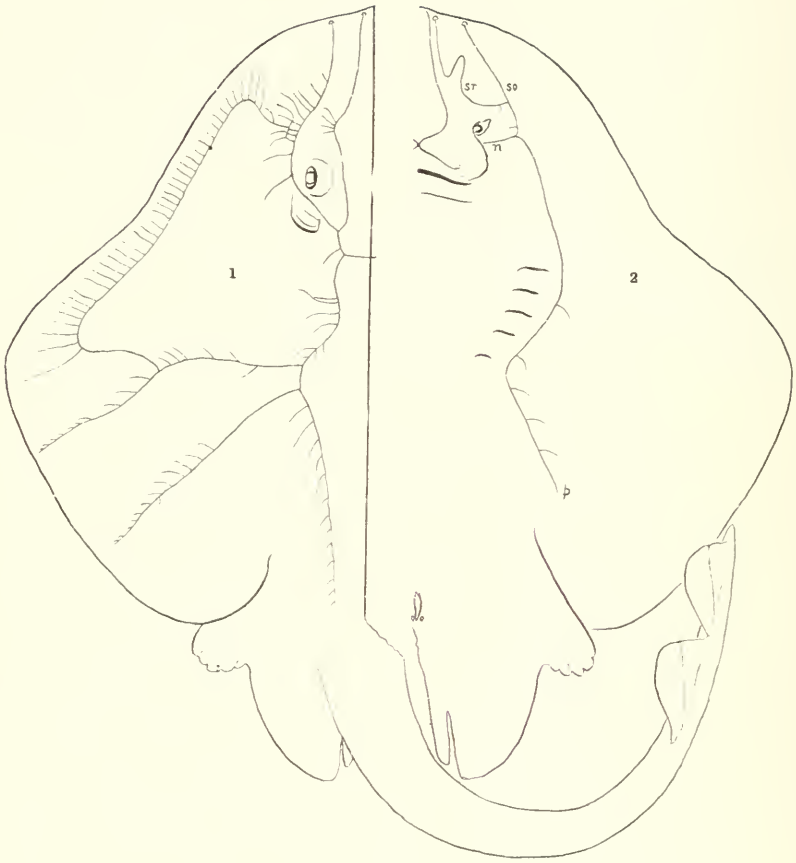

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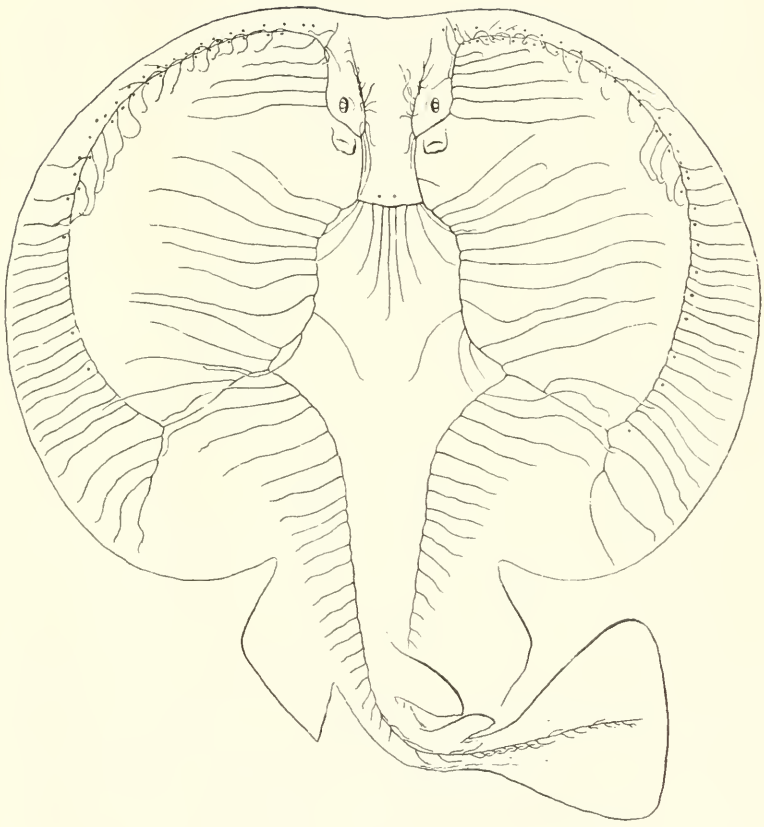
RAIA OCELLATA.



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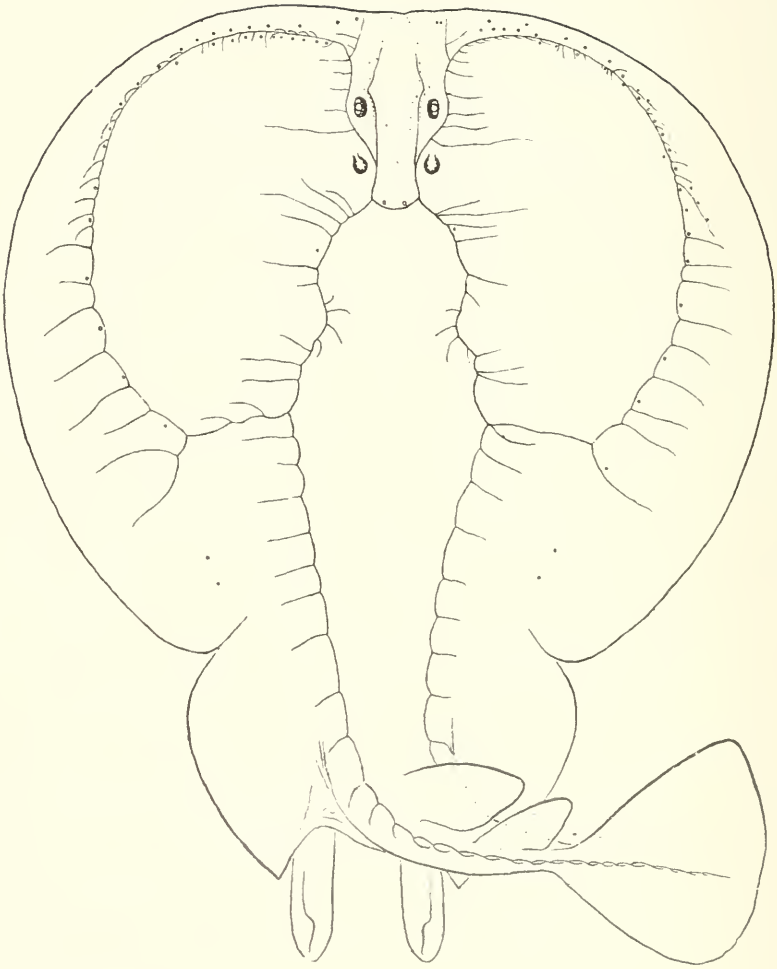
TORPEDO CALIFORNICA.



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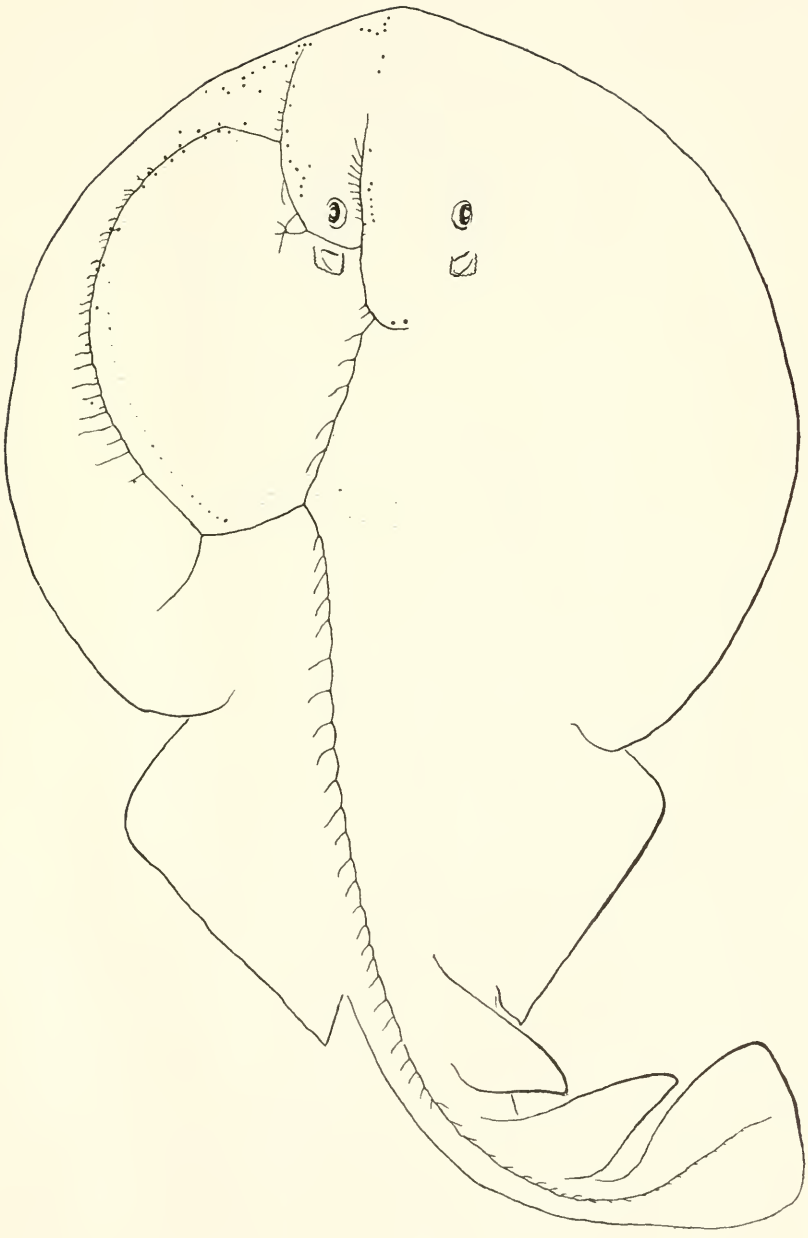
TORPEDO MARMORATA.



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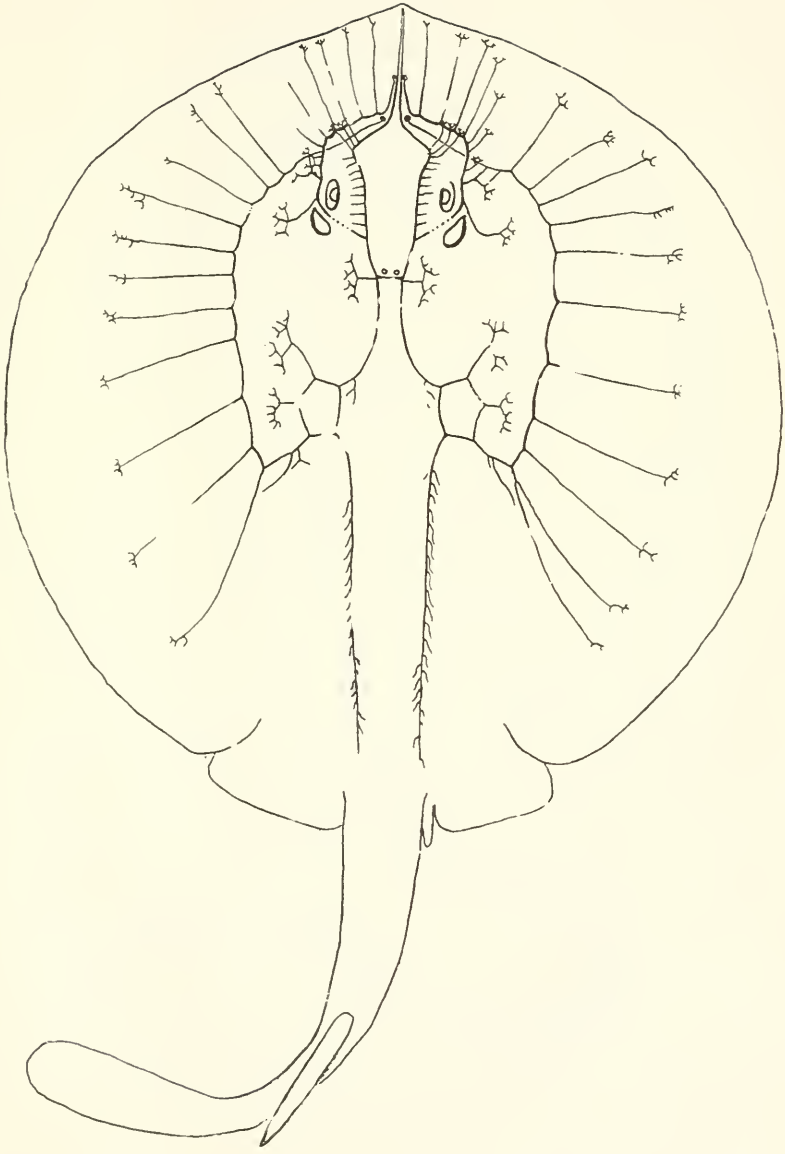
NARCINE BRASILIENSIS.



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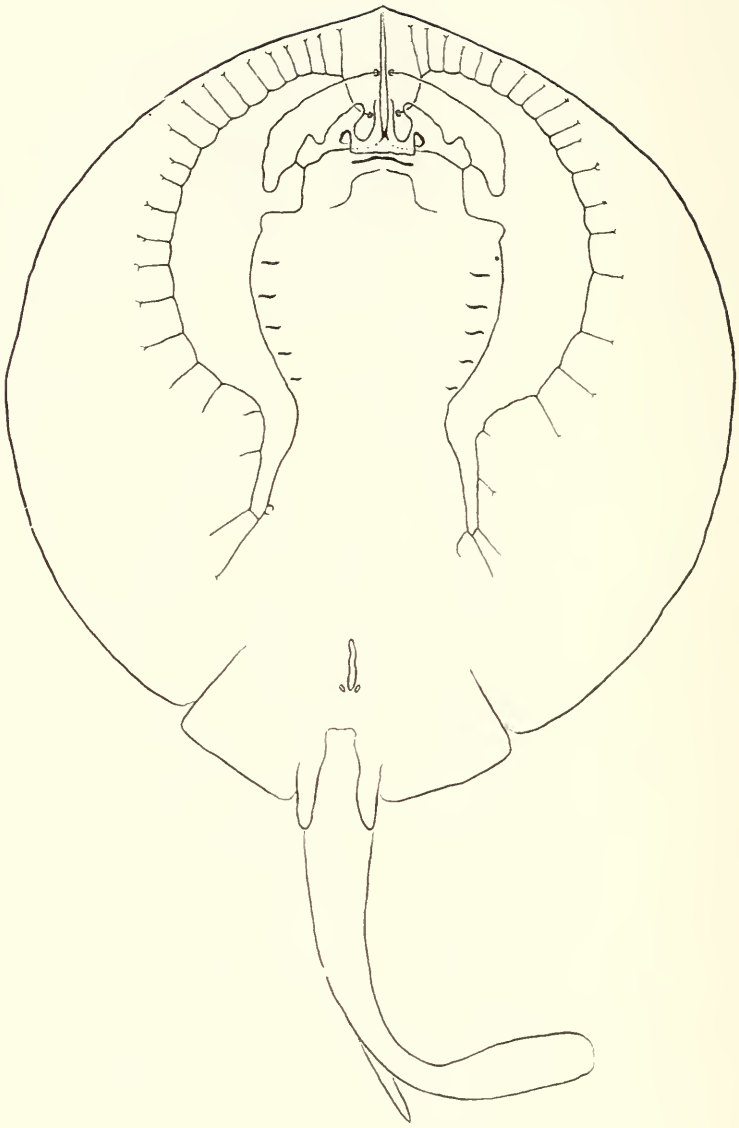
UROLOPHUS HALLERI.



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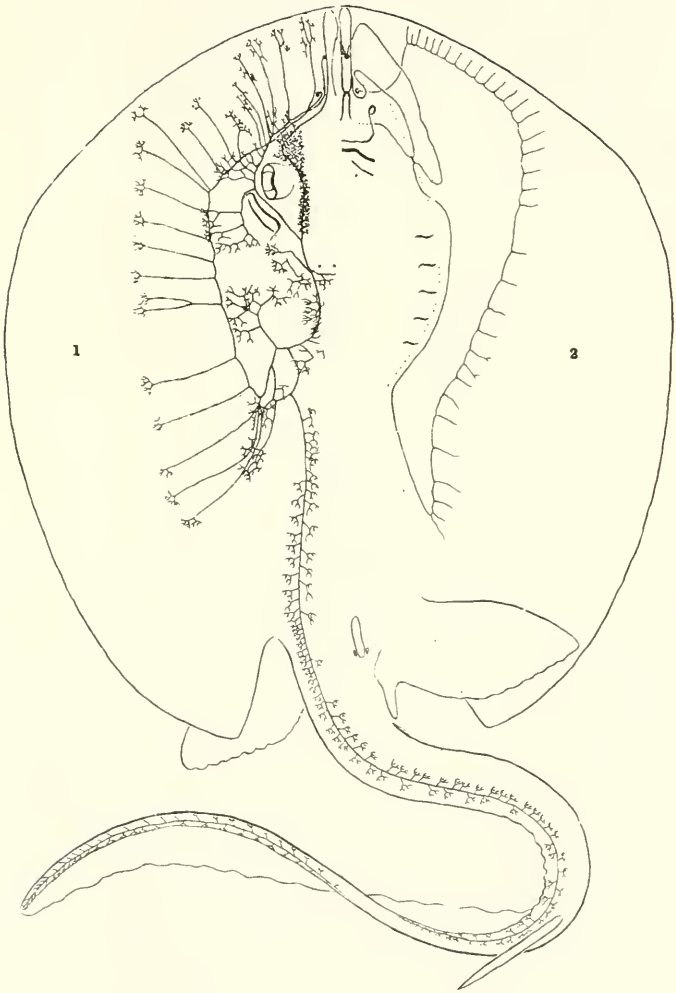

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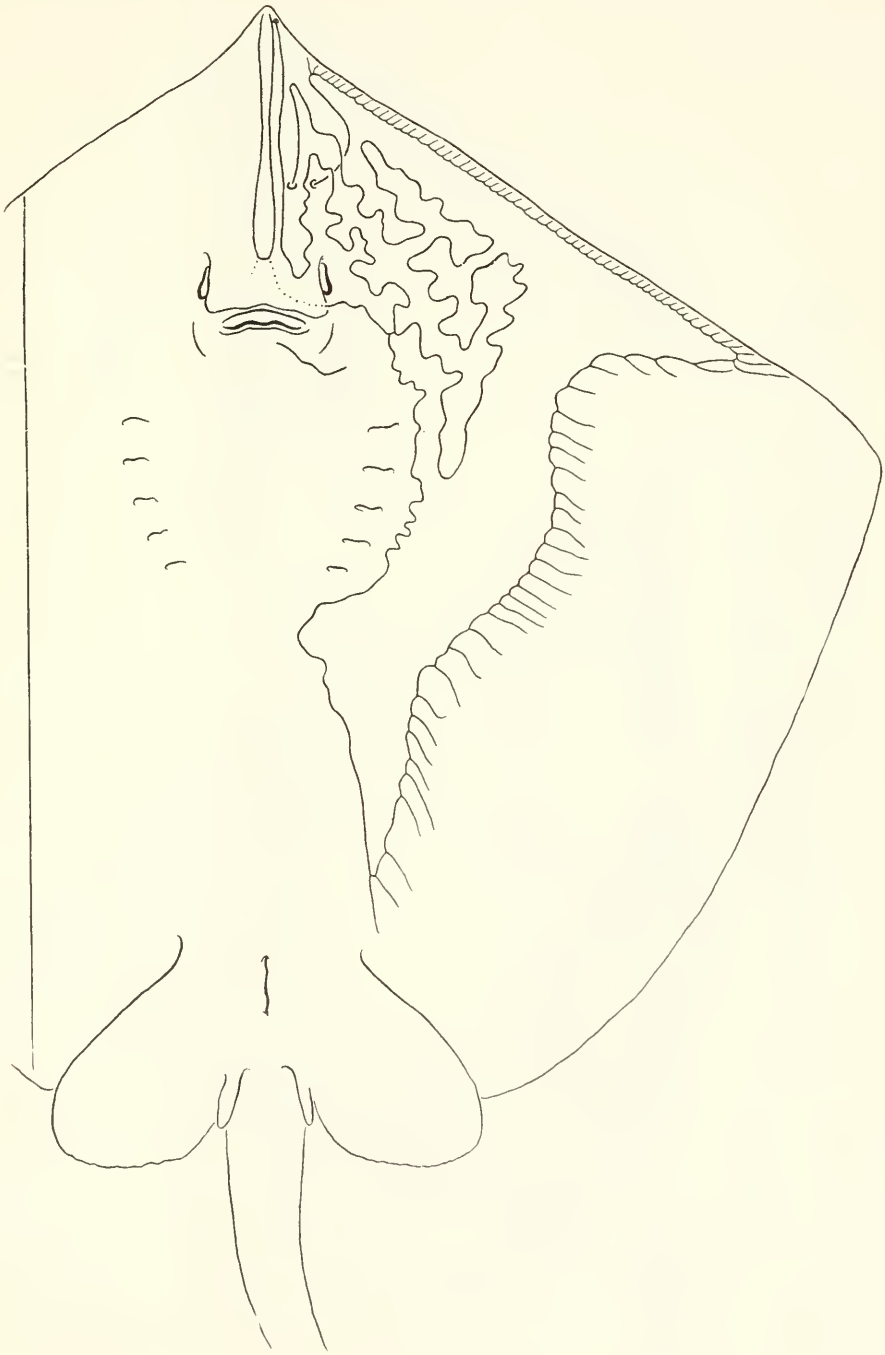
TAENIURA LYMMA.



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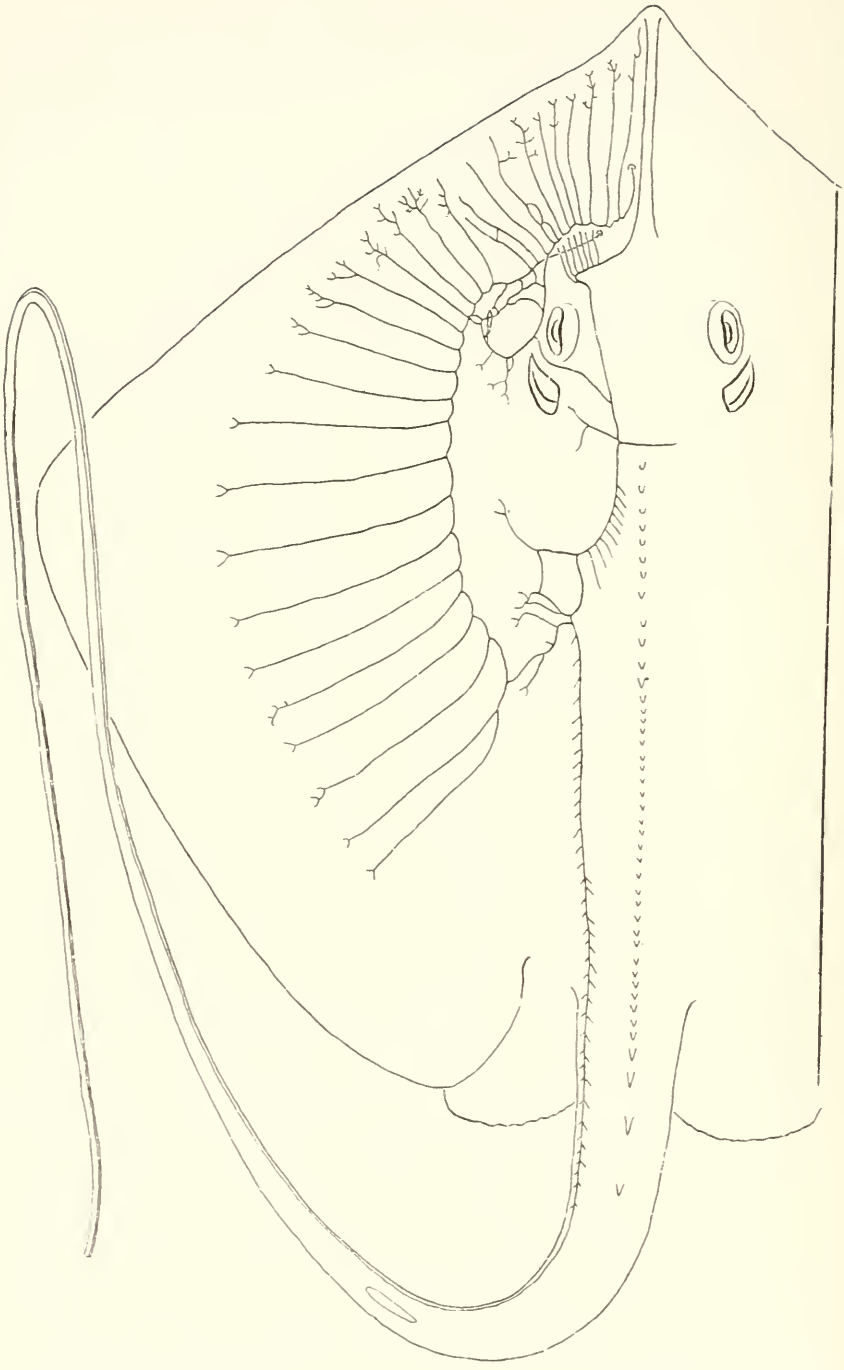
DASYBATUS TUBERCULATUS.



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DASYBATUS TUBERCULATUS.

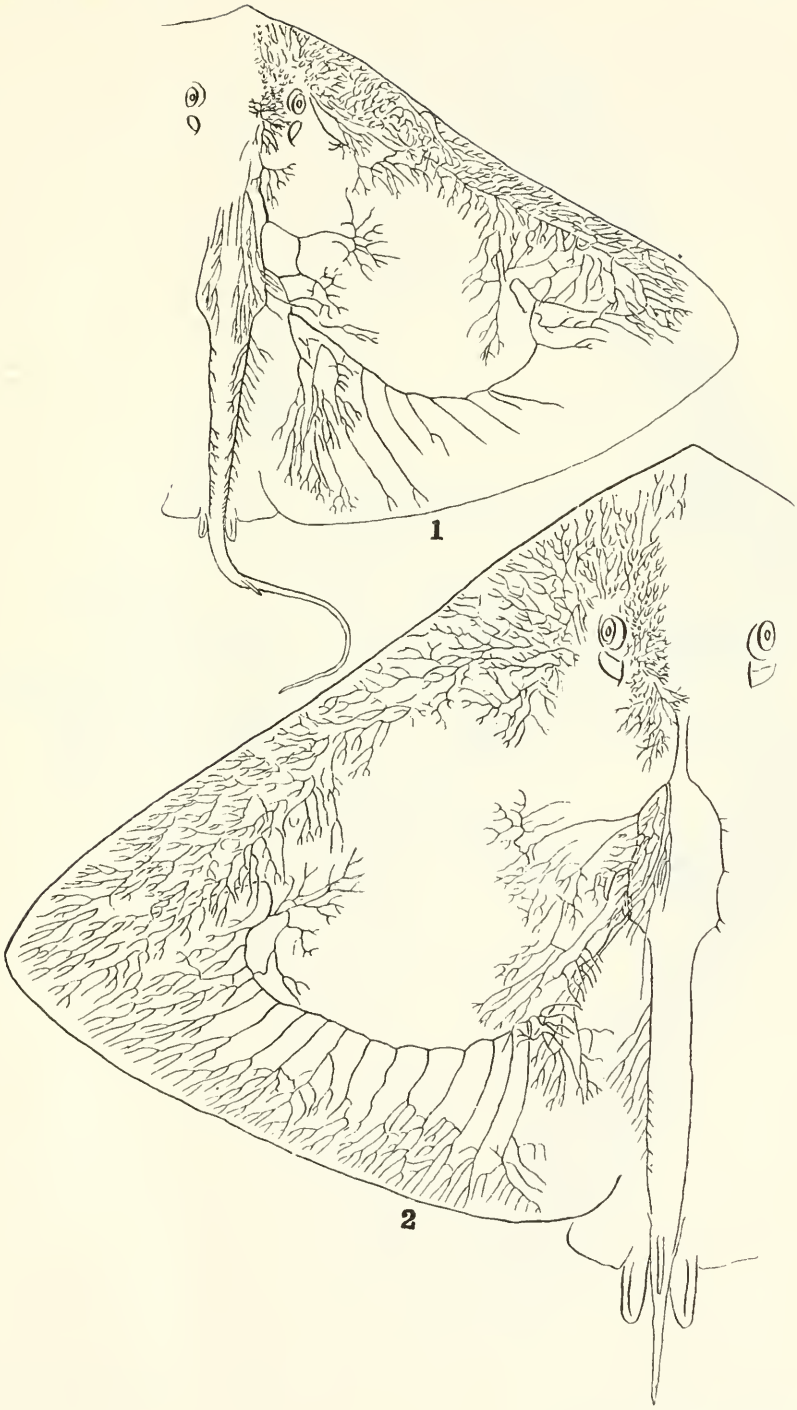
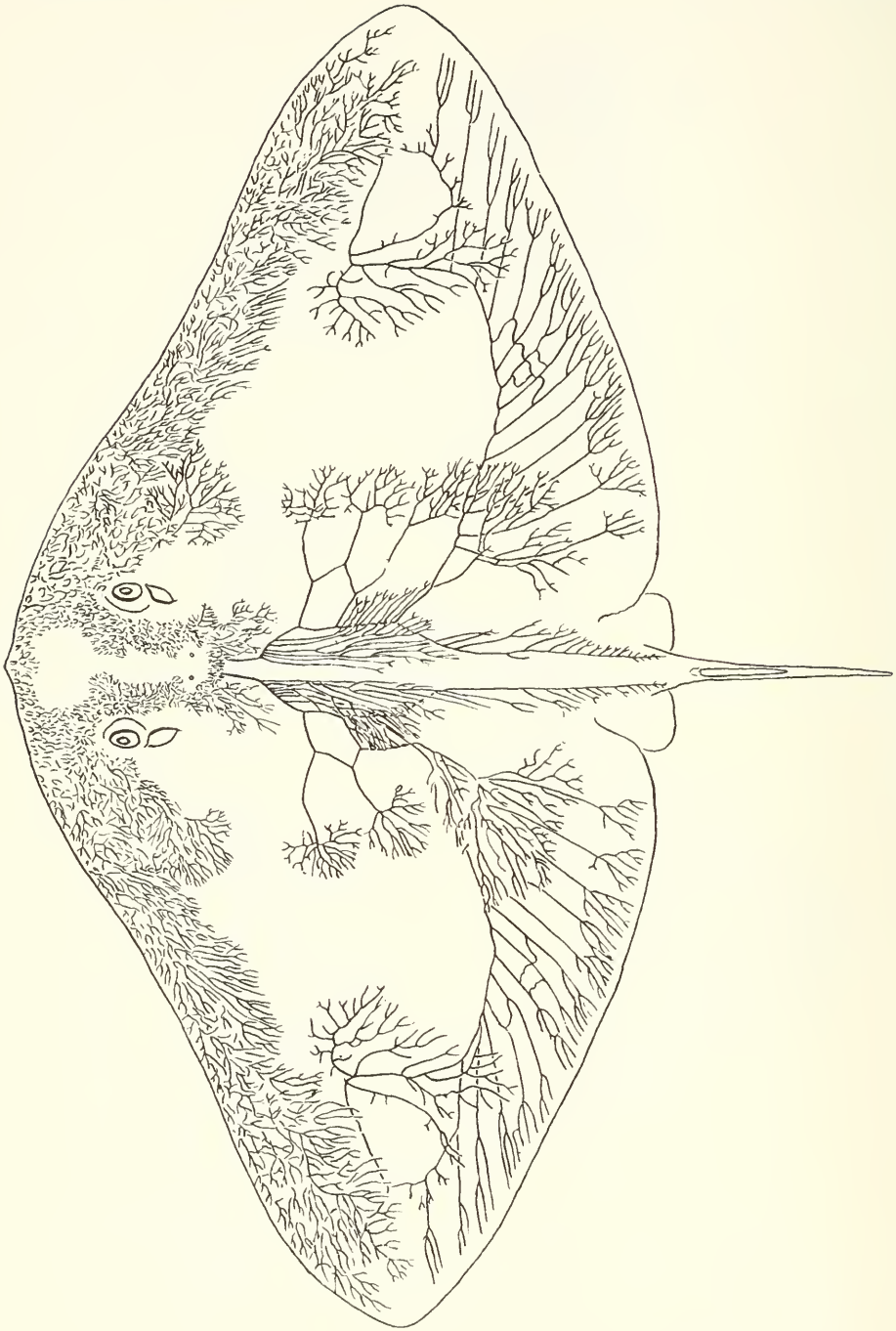


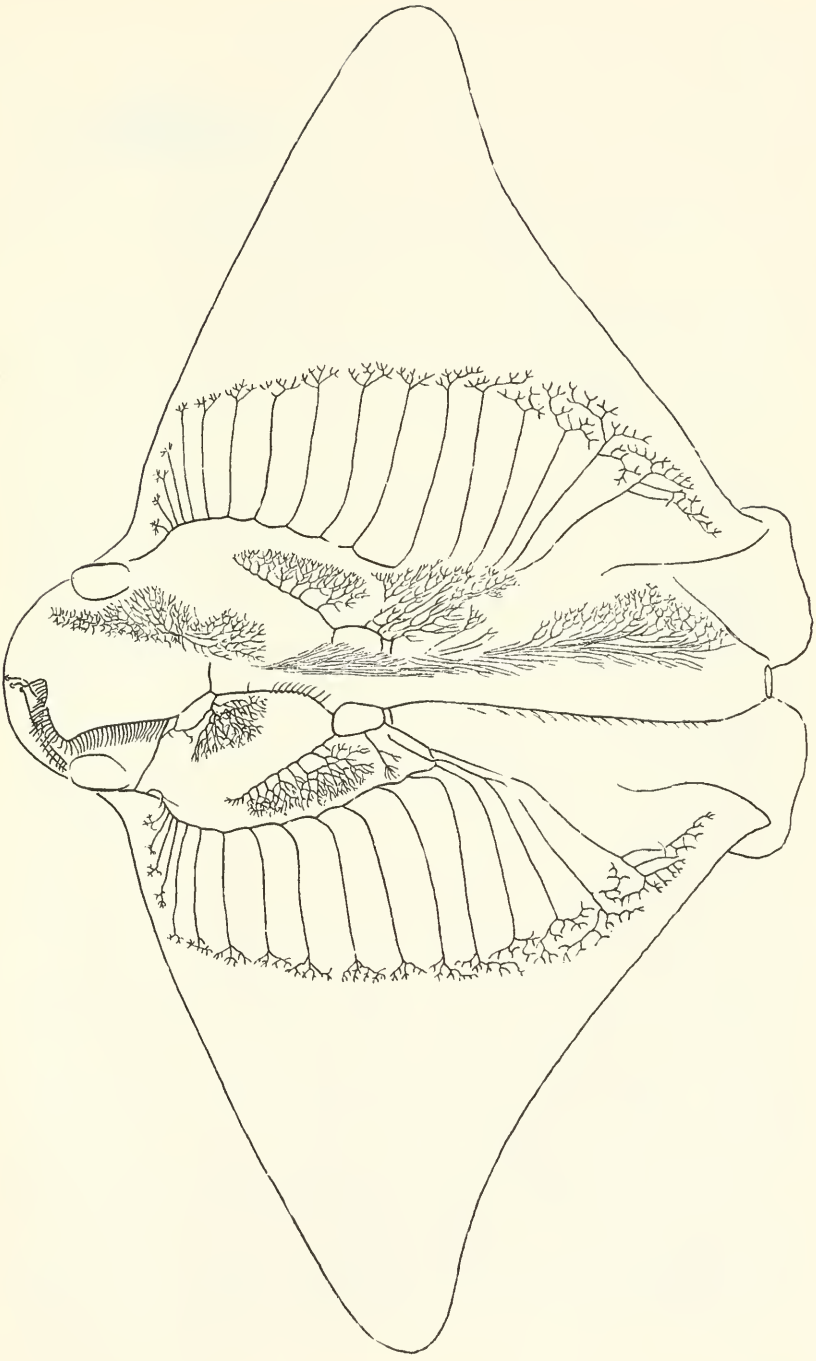
Photo. Lith. of C. S. Punderson & Son, New Haven, Conn.

1. PTEROPLATEA HIRUNDO.
2. PTEROPLATEA MARMORATA.



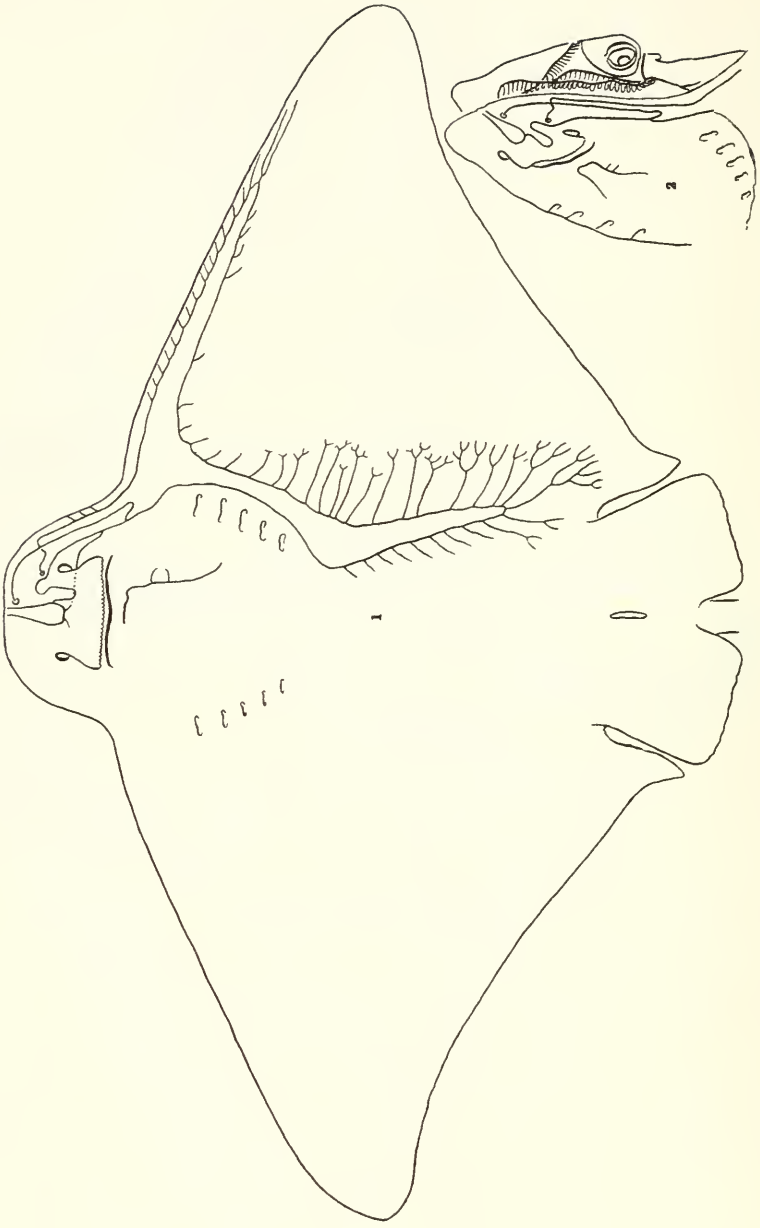
PTEROPLATEA VALENCIENNII.

Photo Lith of L. S Punderson & Son, New Haven, Conn



MYLIOBATIS AQUILA.

Photo Lith. of L. S Punderson & Son, New Haven, Conn



MYLIOBATIS AQUILA.

Photo Lith. of L. S. Punderson & Son, New Haven, Conn.

No. 3. — *The Coral Reefs of the Hawaiian Islands.*

By Alexander Agassiz.

Before giving the results of my observations on the Coral Reefs of the Sandwich Islands, it may be useful to recapitulate the salient points of the older theories of the formation of the coral reefs, from Chamisso's (1815–1818) to Darwin's (1842), as well as the modification of the latter by Dana (1838–1842, 1849), and to enumerate briefly the objections which have been made to the general application of the theory of subsidence to the special cases examined by later investigators, from Agassiz (1851) to the present time.

I need only refer to the earlier views of Forster, who imagined coral reefs to have been built up from the bottom of the ocean, a view which was naturally untenable after the observations of Quoy and Gaymard on the limits of depth at which corals apparently thrive, as well as the later observations of Ehrenberg on the coral reefs of the Red Sea.

Darwin, it should be remembered, examined only the Great Chagos Bank, and based his speculations on the observations he made on this single group, supplementing the knowledge, however, by a most exhaustive analysis of the observations and descriptions of others, and a most thorough examination of the hydrographic charts which had any bearing on the subject. But no naturalist has had opportunities to make a personal examination of the conditions of growth of corals and of coral islands such as have been enjoyed by Dana, as geologist of the United States Exploring Expedition. His Report on Coral Reefs and Islands, published in 1849, contains a full account of his own observations (1838–1842) on the Hawaiian Islands, the Society Islands, the Samoa and Viti groups, and his theories are based upon his own experience, far wider than that of any other writer on the subject. He has therefore drawn but little either from the descriptions of the voyagers of the early part of this century, or from the hydrographic charts, both of which form so essential a part in the Darwinian theory of coral reefs.

An examination of the hydrographic charts of the coral reefs, while interesting, can lead to no sound conclusion. Well as I know the Florida reefs and part of the Bahamas, as well as the majority of the West India coral reefs, I should hesitate to base any general conclusions

upon an examination of these charts, much less to attempt any but very indefinite deductions for local phenomena or conditions.

It seems scarcely necessary to discuss the opinions of Wilkes,[1] who dismisses the whole basis of the theory of coral reefs, besides the special theory of Darwin, and who calmly says: "After much inquiry and due examination, I was unable to believe that these great formations are or can possibly be the work of zoöphytes; . . . I cannot but view the labors of these animals as wholly inadequate to produce the effects which I observed." There seems to be only one critical observation worthy of remark. When speaking of the formation of lagoons he suggests the possibility of the washing influx and efflux of the sea to carry off in the shape of mud or sand, or in solution, the strata underlying the central part of a lagoon. Wilkes further says: "It seems almost absurd to suppose that these immense reefs should have been raised by the exertions of a minute animal, and positively so to explain the peculiar mode of construction by which reefs of an annular shape are formed, when in nine cases out of ten they are of other figures." The last part of his statement seems to have been lost sight of in the discussions on atolls.

In striking contrast to Wilkes's opinions are the observations of Couthouy, one of the naturalists of the United States Exploring Expedition, who published in 1842 his views on the Coral Islands of the Pacific.[2] He suggests that corals are limited in their range of growth by temperature rather than depth, and that wherever this is not below 76° Fahrenheit, then, *cæteris paribus*, they will be found to flourish. Couthouy admits the correctness of the theory advanced by Darwin, and believes the great thickness of the reefs to have been produced by a gradual and long continued subsidence of the original shelf of coral, while the surface was maintained at the same level as at first by the unceasing additions made by the polyps. He also believes that the whole of Polynesia is at present slowly rising, and gives his reasons for believing in a former subsidence of a great continent, mainly based upon the identity of the volcanic and coralline rocks composing the majority of the islands of Polynesia. Couthouy describes the seaward side of the encircling reef of the Paumotu group as representing a succession of terraces or plateaus; the lowest of variable breadth, seldom exceeding one hun-

[1] Wilkes, Charles, Narrative of the United States Exploring Expedition, London, 1845, Vol. IV. p. 268.

[2] Joseph P. Couthouy, "On Coral Formations in the Pacific," Journ. Bost. Soc. Nat. Hist., 1842, p. 66.

dred and fifty feet, and declining rapidly seaward. These terraces as they recede from the sea become shallower and shallower, having at their extremity a sort of steep talus extending to the one next below it. This is probably due to the action of the surf, as the force of the sea becomes less and less where it is broken towards the shore line, though Couthouy is inclined to see in these terraces the effect of subsidence. But as he distinctly says that the outer terraces have only twelve to fifteen fathoms of water on them, about the limit of reef-growing corals, his explanation does not appear satisfactory even in the case of the terrace of Bellinghausen's Island, on which he found twenty-eight fathoms.

It seems much more natural to look upon the channels left, either in the barrier reefs or in atolls, as due to the original inequalities in the level of the foundation of the reef. The corals would naturally reach the surface soonest at the highest point, thus leaving passages which might at particular parts of the reef, and under certain local conditions, be gradually closed by the active growth of the corals, or might, on the other hand, remain open wherever the tides or currents rushed through them with sufficient force to check their increase, or where the silt was deposited in such quantities as to obstruct it.

It is interesting to go back to Kotzebue's Voyage, and to find in the chapter on the Coral Islands, by Chamisso, the following: "The corals have founded their buildings on shoals in the sea; or, to speak more correctly, on the top of mountains lying under water. On the one side, as they increase, they continue to approach the surface of the sea, on the other side they enlarge the extent of their work."[1] He noticed the more rapid growth of the coral where exposed to the action of the surf, and the obstacles to their growth in the middle of a broad reef, due to the amassing of shells and accumulation of coral fragments, and also to the formation of coral land by the cementation of the calcareous sand, gradually increasing in thickness till it is covered by the sea only during certain seasons of the year. He also noticed the formation of reefs more or less circular, with an interior sea, having a depth sometimes of thirty to thirty-five fathoms, which he explains from the action of the natural causes above enumerated.

Dr. Guppy[2] justly says in Nature: "The development of the new theory should be kept in mind. Chamisso seventy years ago advanced the view that an atoll owes its form to the growth of corals at the margin and to the repressive influence of the reef débris in the in-

[1] Kotzebue, Vol. III. p. 331, London, 1821.

[2] H. B. Guppy, Nature, March 15, 1888, p. 462.

terior; but this view gave no satisfactory explanation of the foundation of such a coral reef, and Darwin was driven to his theory of subsidence. The great defect in the way of Chamisso was, however, removed by Murray, who supplied the foundation of an atoll without employing subsidence, and investigation in the Florida Sea (Agassiz) and in the Western Pacific (Guppy) have confirmed his conclusions. The forms of reefs he attributed to well known physical causes. Both Semper and Agassiz have dwelt upon the importance of other agencies, and in our present state of knowledge it will be wisest to combine in one view the several agencies enumerated by them as producing the different forms of coral reefs. On the outer side of the reef we have the directing influence of the currents, the increased food supply, the action of the breakers, etc. In the interior of a reef we have the repressive influence of sand and sediment, the boring of the numerous organisms that find a home on each coral block, the growth of Nullipores, the solvent action of the carbonic acid in the sea-water, and the tidal scour. These are all real agencies, and we only differ as to the relative importance we attach to each. Future investigations will probably add others to the list, besides ascertaining the mode and degree of action of each case."

According to the theory of subsidence, there is no limit to the thickness which a coral reef, rising out of deep water, may attain. It may rest upon rocks of any material situated in a region of subsidence, while naturally it would extend mainly vertically, its horizontal width being comparatively slight. According to the other theory, which does not call upon subsidence to explain the formation of barrier reefs or of atolls, the base of coral reefs, whether atolls or barrier reefs, may be any plateau or eminence, either volcanic or the product of accumulations of limestone banks, which have reached the requisite height for the growth of corals. The presence of such limestone banks and of eminences, either volcanic or other, which have reached the level at which corals will flourish is nowhere better exemplified than in the West Indian region, where we find atolls, barrier reefs, and fringing reefs in a region which is eminently one of elevation. In an area of elevation we may have comparatively thin reefs, forming a mere casing to the core upon which they have grown, as Guppy has shown in the case of one of the Solomon Islands.[1]

Mr. J. J. Lister, the naturalist of H. M. S. Egeria, Commander Aldrich, describes Christmas Island as being a succession of horizontal terraces, marking the pauses of its gradual elevation during which a

[1] Nature, December 29, 1887, p. 203.

fringing reef was formed.[1] There was a cap of coral limestone over the whole island; the very top of the island, twelve hundred feet high, being a block of worn and undermined coralline limestone, then tiers of cliffs intervening between the top and existing sea cliffs. "Christmas Island thus appearing to be a remarkable instance of the complete casing with coral of an island, which, from the time that its first nucleus came within the reef-building zone, has been steadily subjected to a movement of upheaval varied by pauses, during which the cliffs were eroded by the sea."

That the volcanic nucleus has not been exposed is undoubtedly due, as has been suggested by Guppy,[2] to the fact that the upheaved island has not been exposed to denuding agencies for a sufficiently long period of time.

Murray,[3] who had unusually good opportunities for examining numerous coral reefs of the Pacific, published a remarkable paper on the formation of reefs in the Proceedings of the Royal Society of Edinburgh, in which he gives an explanation of the formation of channels between barrier reefs and the mainland band, and of the lagoons of atolls, based upon the solvent action of sea-water saturated with carbonic acid upon coral limestone. That this solvent action is a powerful factor in corroding the surface of coral reef, and carrying off surplus limestone in solution is not to be denied, but to consider it the principal cause of the formation of lagoons and of channels between barrier reefs is perhaps pressing the theory too far. It undoubtedly has acted in many cases powerfully enough to corrode the whole surface of reefs exposed to action of water so saturated with carbonic acid. I would refer specially to the surface of reefs like the fringing reefs of Honolulu, the corroded breccia reef rock found at many points of the Keys of Florida, and the evidence of the same action to be found on the shore deposits of coral along the whole northern coast of Cuba, where the shore reef exists parallel with the great Cuban barrier reef. Similar action, of course, is taking place constantly in limestone districts, through which waters saturated with carbonic acid percolate, forming caves and other cavities so characteristic of these formations.

[1] A similar condition of things exists at Barbados, where the volcanic reef centre crops out only on the summit of the island, and the sides of the cone are covered with coral reef terraces, which are one of the most characteristic features of the island as seen from the sea. A. Agassiz, Three Cruises of the Blake, figs. 39, 46.

[2] Nature, January 5, 1887, p. 223.

[3] Murray, John, Proc. Royal Soc. Edinb., 1879–80, p. 505.

Wherever in that region the fringing reef has attained any considerable width, we find that upon the portion nearer shore, where the corals once flourished, they have died because the extension of the reef towards the shore has excluded them from contact with the fresher sea-water outside. This part of the reef has been corroded and eaten off, or was dissolved, as Murray suggests, by the action of the carbonic acid held in sea-water, which absorbs a large amount of carbonate of lime.

But it should not be forgotten that this solvent action of carbonic acid in sea-water cannot be considered as the chief agent in the formation of barrier reefs. Take, for example, the case of the Florida reefs, or that of the great barrier reef of Australia. The former are so far from the neighboring chain of keys, and the latter so distant from the adjacent mainland, that such an explanation of the presence of the channel separating the one from the keys, the other from the shore, would involve the solution and disappearance of the reef itself.

We are inclined to look upon the depth and extension of the ridge or plateau upon which a barrier reef first establishes itself as the chief cause of its growth and final form. Such a plateau having reached the level at which corals flourish, the reef begins to grow, and its distance from the mainland or from the adjacent islands is thereafter determined by the contour lines of the submerged extension of the land seaward or landward. Nevertheless, the effect of the relatively clear or muddy water on the sea and land faces of the incipient barrier reef cannot have failed to exercise an important influence on its seaward or landward development.

Murray [1] clearly shows that the solution of dead carbonate of lime shells and skeletons by sea-water is as constant as its secretion by living organisms. He considers it probable that on the whole there is more secretion than solution, and that there is at the present moment a vast accumulation of carbonate of lime going on in coral areas no one familiar with the subject will deny. This secretion diminishes with the depths, while the rate of solution perhaps increases under pressure. He compares it to the action of aqueous vapor in the atmosphere over land surfaces. When precipitation is in excess of evaporation fresh-water lakes are formed ; when evaporation, on the contrary, exceeds it, salt lakes are formed in inland drainage areas.

The discussion on the theory of solution which has taken place in "Nature" between Reade and other geologists, does not appear to cover the ground. The objections are mainly made by investigators who know

[1] Nature, March 1, 1888, p. 414.

little of coral reefs from their own observations, some of whom have ignored or flatly denied facts which can hardly be dealt with in so summary a fashion.

According to Reade,[1] it seems very evident that if we accept the dissolution theory for the origin of coral lagoons, it seems impossible to believe in the building up of calcium carbonate, or volcanic platforms, or other peaks, from varying and unknown depths to the levels necessary for the growth of coral reefs. If, on the other hand, we believe that platforms are so built up, it appears equally destructive of the dissolution theory of lagoons.

In "Nature" of September 21, 1880, Mr. Reade says: "I think the theory Mr. Murray sets forth, — that the cones or peaks on which he considers atolls have been formed have been levelled up by pelagic deposits, and thus brought within the limits of reef-building coral growth, — a very far-fetched idea."

In the same journal, Darwin says: "I am not a fair judge, but I agree with you exactly that Murray's view is far-fetched. It is astonishing that there should be rapid dissolution of carbonate of lime at great depths and near the surface, but not at intermediate depths, where he places his mountain peaks."

It is surprising that Reade[2] should have attempted to throw doubt on the existence of calcareous submarine banks. The submarine banks are not, as Mr. Reade seems to think, due to the tests of the pelagic fauna alone. A submarine peak is not built up by the pelagic fauna, but it is built up by the carcasses of the Invertebrates that live upon it, and for which the pelagic fauna serves in part as food. Certainly, the amount of limestone and shells of pteropods alone in some regions is very much larger than any estimate made by Mr. Reade. The large number of well known limestone banks of great thickness and extent should make such a discussion unnecessary.

The "pelagic cemetery" is farther down, and not on the surface, and I would refer Mr. Reade to my article on the Florida Reefs, in the Memoirs of the American Academy of Arts and Sciences, 1883, as well as to the "Three Cruises of the Blake," for such proof as has thus far been obtained regarding the existence of these huge masses of limestone banks, eminently fitted, as I think I have shown, to form the base of such coral reefs as those of the West Indies, of Florida, of the shores of Cuba, and of the great Alacran and other reefs on the Yucatan Bank.

[1] T. Mallard Reade, Nature, March 22, 1888, p. 489.

[2] Nature, April 5, 1888, p. 535.

The following are the principal experiments which have been recorded regarding the solvent action of sea-water on corals. According to Mr. Robert Irwine,[1] dead or rotten coral of several species of Porites, exposed to sea-water of 1.0265 specific gravity, and of a temperature of from 70° to 80° Fahrenheit, was found to be soluble to the extent of 5 to 20 ounces to the ton. We have no data to show how far this capacity of solution is in excess of the deposition of limestone due to the corals themselves, or to the sand and débris carried into the lagoons or the inner part of the reefs. No observations have been made regarding the amount of carbonate of lime existing in lagoons, and in the sea-water on the sea face of a reef.

Mr. W. G. Reid, in a paper read before the Royal Society of Edinburgh, February 6, 1888, observed that the solubility of carbonate of lime increased with pressure.

Mr. James G. Ross[2] detailed in "Nature" other experiments showing a considerable amount of solution. In a species of Oculina 0.0748 gramme was lost, from a specimen weighing 16.3164 grammes, in twenty days. In another case, 0.1497 gramme was lost in thirty days by a mass of Madrepora weighing 15.334 grammes. The above experiments would both indicate the possibility of a very material deepening of a lagoon by the solution of the coral. At such a rate of solution, a lagoon four miles in diameter might be deepened one fathom in a century.

The rotten condition of the old shore reef of Havana,[3] completely honeycombed as it is, shows how rapidly limestone is acted upon by sea-water. The rotten reef rock of the Everglades, soaked by brackish water, which is often accumulated in large bodies behind the old reef ranges, has been described by Professor Agassiz. This water, saturated with carbonate of lime, often rushes out with considerable volume after a storm, and produces great havoc with the shore fishes of the adjoining reef. Their dead bodies often line the shores of the Florida reefs for miles, when there has been such an outburst of water saturated with carbonic acid. The existence off shore of bands of sea-water similarly saturated with carbonic acid may explain the great destruction of fishes which so often takes place in fishing vessels carrying their catch from the Florida Reef to Havana. It will have been noticed by all who have ever seen a coral sand beach, or a breccia beach, or a beach composed

[1] Nature, March 15, 1888, p. 461.

[2] Nature, March 15, 1888, p. 462.

[3] See Three Cruises of the Blake, Fig. B, p. xii.

of larger fragments of coral and reef limestone, that the constituent parts of the beaches were, as could easily be seen by the eye, invariably corroded far beyond the condition to which the sand or breccia, or larger fragments, could be reduced if merely subjected to the triturating agency of the rollers. An analysis made by Prof. F. W. Clark, the chemist of the United States Geological Survey, of such fragments, either as sand or in all intermediate stages up to fragments of coral, or coral limestone, showed very clearly that the chemical composition of the pieces was practically the same.

The only analysis known of the chemical constituents of the sea-water of the lagoon of an atoll is given as determined by Messrs. Stillwell and Gladding,[1] from which it would appear that the amount of chlorine was considerably larger than the amount given in the latest analysis of Dittmar, and that the water of the lagoon is fresher than that of ocean water.

It may not be out of place to mention here, that there is a most excellent figure and plan of an atoll in an account of Caroline Island,[2] by Prof. E. S. Holden, the director of the American Eclipse Expedition of 1883. Not only is the description of the atoll admirable, but the illustrations of the various parts of the island are most characteristic, including one of the best figures perhaps of a bird's-eye view of an atoll. A map also accompanies the description, but unfortunately no soundings are given.

Lagoons without openings are perhaps older lagoons, in which the openings have from local causes been gradually closing, and from the porous nature of the surface coral rock there still remains a chance for the exchange of waters from the interior to the exterior of a reef.

Jukes,[3] who in 1845 surveyed the Great Barrier Reef of Australia, came to the conclusion that the "northeast coast of Australia has either been slightly elevated, or that it has at least not suffered any depression during a long period of time." From this he has satisfied himself that, wherever we find coral reefs rising abruptly from unfathomable depths, they must necessarily have been produced by the depression of the sea bottom, the corals building on upwards as the bottom was slowly sinking, so as to keep the upper portion of the reef always within the required depth. The depression of the bottom, according to this view,

[1] Mem. Nat. Acad. of Science, Vol. III. p. 96.

[2] Report of the Eclipse Expedition to Caroline Island, May, 1883, Mem. Nat. Acad. of Science.

[3] Jukes, J. B., Narrative of the Surveying Voyage of H. M. S. Fly, Vol. I. p. 311.

has occupied a far longer period than that during which the northeast coast was either stationary, or had been slightly elevated. He urges the parallelism of the outline of the Great Barrier Reef with that of the northeast coast as evidence that the circumstances which modified the outline of the coast likewise determined the general outline of the reef, while subsidence would most assuredly produce the results observed on the northeast coast of Australia if the rate of growth of corals were absolutely identical with that of the subsidence of the bottom of the sea. With our present knowledge of the mode of coral reef formation, it seems unnecessary to explain the existing state of things by a subsidence coincident in rate with the growth of corals, when observation plainly shows us that there has been only a slight elevation or a stationary condition of the coast line. Starting from the conditions Jukes imagines to have existed before the subsidence took place, only leaving the coast nearly at its present level, we can imagine a fringing reef to have been formed slowly, and to have little by little extended seaward, advancing more slowly as the depth increased, while the talus for the upper limits of coral grew, it increased in thickness, and to have ended in a barrier and inner reef with channels very much like the reef we find to-day.

Is it credible that, along the whole length of the northeast coast of Australia, the subsidence should, for a length of over one thousand miles, be so nearly identical in amount as to have ended in forming parallel to it the Great Barrier Reef? The same question is one which must be answered not only for Australia, but for all the atolls and barrier reefs in the Pacific and other regions where such reefs exist.

We have all over the world many positive proofs of the elevation of the land, sometimes on a gigantic scale, as in South America, for instance, up to nearly three thousand feet. Neither can we deny that there are many points, especially in the Pacific Ocean, where are to be found areas of subsidence; but it is by no means proved that this subsidence has been the main cause of the formation of atolls or of barrier reefs. In fact, all the later investigations of coral reefs have, without exception, rejected Darwin's theory of subsidence as explaining the formation of reefs, and they have looked to other causes, which seemed to them more natural, as probably more efficient in the growth of reefs. The question is not whether subsidence has taken place even in the areas where atolls or barrier reefs occur, — this may be considered as proved, — but whether this subsidence has absolutely kept pace with the rate of growth of corals. It is remarkable that Darwin, who is so strongly opposed to all cataclysmic explanations, should in the case of the coral reefs cling

to a theory which is based upon the disappearance of a Pacific continent,[1] and be apparently so unwilling to recognize the agency of more natural and far simpler causes.

Granting that during the secondary period the great East India islands were connected with Asia, and that there had been in the early tertiary period a great subsidence, which may have extended throughout some parts of the Pacific to the time of the formation of modern coral reefs, — granting even that the summits of the islands now existing indicate plateaus upon which the various archipelagos of the Pacific are based, and point to a former extent of land far greater than now projects above the surface of the sea, and also that the islands of the Pacific mark a general subsidence along a line extending from the southeast to the northwest, as is urged by Dana, — yet there is nothing in all this to show that the subsidence has been the main cause of the formation of atolls and barrier reefs, while the existence of such a subsidence in its turn derives its strongest proof, with many writers, from the existence of atolls and barrier reefs. As long as we can in so many districts explain the formation of atolls and of barrier reefs by other causes, fully sufficient to account for the numerous exceptions to the theory of Darwin, which have been observed by so many investigators since the days of Darwin and Dana, it seems unnecessary to account for their presence by a gigantic subsidence, of which, although we may not deny it, we can yet have but little positive proof.

Dana has been led to reconsider the earlier and later observations, and has given his results in the American Journal of Science.[2] He most distinctly rejects Darwin's hypothesis, that the slow subsidence upon which he counted to form atolls and barrier reefs from fringing reefs involved the whole central Pacific, besides other large areas, a Pacific continent having disappeared through subsidence.

Whether subsidence is going on now, or has ceased after the formation of atolls, which he ascribes to it, seems immaterial. The point at issue is, how far is it possible for atolls and barrier reefs to begin in an area of limited extent without a constant alternation of elevation and subsidence. It seems to me that the rocky islets dotting the interior of Kaneohe Bay could as well be cited as proof of subsidence, as the rocky

[1] This part of the theory of Darwin, which seems a natural corollary of his explanation of coral reefs, is most emphatically rejected by Dana, Am. Journ. of Science, Vol. XXX. p. 90, 1885, and previously also in his Geology of the Exploring Expedition, in 1849.

[2] Am. Journ. of Science, August, 1885, p. 89, and September, 1885, p. 169.

islets which dot the great lagoon-like waters of the Gambier group, "leaving scarcely any doubt in the mind that the islets were the emerged points of sunken lands; and if this is evidence of subsidence, then the atoll [of Keeling] which he [Darwin] examined was proof of further subsidence, that is, one that had continued to the disappearance of the sinking peaks." This is the proof which Darwin believed to be almost certain evidence of subsidence.

Dana adds, as an argument in favor of subsidence, the existence of deep fiord-like indentations in the rocky coasts of islands, both those inside of barriers and those not bordered by reefs. Certainly this is a most unsafe method of reasoning, unless accompanied by sounding in the fiords to show the continuation of the slope of erosion. As to the nonexistence in the ocean now, and the extreme improbability of the existence at any time, of submarine volcanoes or chains of mountains having their numerous summits within a hundred feet of the surface, which has been a favorite argument against the possibility of a volcanic base for reefs, the recent deep-sea soundings of the Atlantic in volcanic districts, like that off the west coast of Africa by the Talisman, have shown the existence of numerous peaks and submarine banks, which in the track of oceanic currents would soon be built up to the level at which corals can thrive, and produce the very conditions denied by Darwin. A similar state of things has been developed by the soundings of the Blake in the West Indies.

Dana mentions the great width of a reef as an indication of subsidence. I am unable to see the force of that argument. It seems merely to indicate the great length of time which has elapsed since it began to build. We might take for granted the evidence of subsidence as deduced by Dana for the Tahitian group and for the Samoan group, for instance, and yet we should not have the proof that this subsidence was coexistent with the formation of the different kinds of reefs.

If, as is supposed, we can have submarine banks of limestone formed upon volcanic mountains or other steep slopes, the steepness of the slope off the coral reef, does not argue anything in favor of subsidence. I do not see that the large débris offer positive proof of subsidence, if they have, as Murray supposes, gradually rolled down the steep talus of the sea face of the reef, and have, as is certainly the case in the Sandwich Islands, formed the surface, which may be of great thickness. Dana infers, from the statement I made in regard to the former connection of the Windward Islands[1] with South America, that there has been a sub-

[1] Bull. Mus. Comp. Zöol., 1879; Am. Journ. of Science, XVIII. 230, 1880.

sidence. It may also be that erosion has been amply capable of washing away the land connections, and forming the banks on which the islands rest as it were.

As to there not being any mound now approaching the ocean surface in the western border of the Gulf Stream, the past history of the Gulf Stream itself, of the Florida Plateau, and of the formation of the Keys of Florida and of the present reef, seem to me to furnish just such a foundation for reef-building as is required by Dana. The Mosquito Bank, the Yucatan Bank, and the smaller banks between Honduras and Jamaica, are all proof that immense limestone banks are forming at any depth in the sea, or upon pre-existing telluric folds or peaks, constituting banks upon which, when they have reached a certain depth, corals will grow. Is it claiming too much for erosion to say that some of the volcanic peaks may have been washed away and swept into the sea? Certainly this is not the case in any region where there is a rainy season. The Sandwich Islands themselves, greatly modified as they have been by erosion, furnish the best evidence that isolated peaks may have completely disappeared. A careful perusal of Dana's own account of the effect of erosion on their topography, and of Captain Dutton's later examination, shows how powerful a factor they regard erosion to have been in these islands. And if we go farther towards the equator, or to the region of cyclones and tornadoes, the action of erosion will be found to be far more powerful than in the Sandwich Islands, which are on the very edge of the rainy season district.

It is somewhat surprising that, in the discussion which has lately been carried on in the English reviews,[1] by the Duke of Argyll, Huxley, Judd, and others, regarding the new theory of coral reefs, no one should have dwelt upon the fact, that, with the exception of Dana,[2] Jukes,[3] and others who published their results on coral reefs soon after Darwin's theory took the scientific world by storm,[4] not a single recent original investigator of coral reefs has been able to accept this explanation as applicable to the special district which he himself examined. It is interesting to note that, however widely Darwin's theory was accepted and spread in all text-books of Geology, neither L. Agassiz,[5]

[1] "Nature" and "Fortnightly Review."

[2] Dana in 1838–1842; "Corals and Coral Reefs," in 1872.

[3] Jukes in 1845, Narrative of the Surveying Voyage of H. M. S. Fly, Vol. I. p. 31, 1847.

[4] Darwin in 1842, "The Structure and Distribution of Coral Reefs"; Darwin's Coral Reefs, 1874, 2d edition.

[5] Agassiz, L., U. S. Coast Survey Reports, 1851 and 1866; also Methods of Study (popular sketch). See Vol. VII., Mem. Mus. Comp. Zoöl.

who examined the Florida Reefs in 1851, nor Joseph Leconte,[1] his assistant, who published subsequently views somewhat different from those of L. Agassiz, nor E. B. Hunt,[2] who promulgated a theory of the formation of the Florida Reefs, nor A. Agassiz, who spent several seasons in parts of Florida, on the Florida Keys, and on the Tortugas, was able to accept Darwin's theory as offering an explanation of the formation of the great reef extending from the Tortugas to Cape Florida.

Agassiz, while in general he accepted Darwin's theory as applicable to atolls, yet gave, in 1851, (Report of United States Coast Survey, republished with additions in the Memoirs of the Museum of Comparative Zoölogy,) an account of the Florida Reefs, showing the living reef outside of the lagoon, and its position with reference to the line of Keys. I subsequently gave a number of sections of the same reef from the Coast Survey maps,[3] showing the formation of a barrier reef actually going on, where the reef foundation grows lower and lower, and where we need not have recourse to the theory of solution for the formation of a lagoon. The lagoon we can actually trace from its broadest point at the Rebecca shoal, where the reef is submerged, to its narrowest point at the northern extremity of the reef.

Leconte accepts the theory of subsidence as a satisfactory explanation of the formation of atolls in the Pacific Ocean; but in Florida, which he visited with Professor Agassiz in 1851, he agrees with the latter in his account of the formation of a barrier reef where there has been no subsidence, and then he points to the Gulf Stream running parallel with the trend of Florida, as the agent which has deposited the great mass of the Florida bank below the level at which corals can grow. But there is no evidence that the Gulf Stream ever ran in the direction assumed by Leconte. Agassiz also accepted the theory of subsidence as generally explaining the formation of the different kinds of coral reefs, though in his account of the formation of the Florida Reef he does not go beyond the depths at which reefs grow, and says nothing of the substructure or foundation rock. In February, 1878,[4] I called attention to the exist-

[1] Am. Jour. Science, XXIII., May, 1857, p. 46, "On the Agency of the Gulf Stream in the Formation of the Peninsula and Keys of Florida," by Joseph Leconte; also Elements of Geology, New York, 1878.

[2] Hunt, E. B., Am. Jour. Sci., 1863, Vol. XXXV. p. 197.

[3] In the Tortugas and Florida Reefs, Memoirs of the American Academy, Vol. XI., 1883.

[4] Agassiz, A., Letter No. 1 to C. P. Patterson, Supt., on the Dredging Operations of the U. S. Coast Survey Steamer Blake, Bull. Mus. Comp. Zoöl., V., No. 1, 1878.

ence of a great atoll, Alacran Reef, on an area of elevation on huge limestone banks such as those of Yucatan.

Leconte insists on the fact that the Florida Reef, a true barrier reef, has been formed where there could not be any subsidence, as continuous increase of land is inconsistent with subsidence. According to Darwin, barriers and atolls always show a loss of land, only a small portion of which is recovered by coral and wave agencies, while on the Florida coast, according to Leconte and Agassiz, there has been a continuous growth of the peninsula by coral accretion, until a very large area has been added.[1] He attributed the formation of successive reefs to the successive formation of the depth condition necessary for coral growth, and this latter, in the absence of any evidence of elevation, to the steady building up by sedimentary deposits and extension southward of a submarine bank within the deep curve of the Gulf Stream as it bent its way round the west coast of Florida.[2] The formation of barrier reefs instead of fringing reefs on a coast which has certainly not subsided, he attributes to the shallowness and muddiness of the bottom along this coast. Only at a distance of twenty to forty miles, when the depth of twenty-five fathoms is reached, and when, therefore, the bottom is no longer changed by the waves, the conditions necessary for coral growth could be found, and here a line of reefs would be formed, limited on one side by the depth, on the other by the muddiness, of the water.

According to Leconte the building up of Florida and of the Keys was due to the co-operation of several agents : —

1. The Gulf Stream building up and extending a submarine bank within its loop, but not in the position assigned to it by Leconte.

2. Corals building successive barriers on the bank, as the latter was pushed farther and farther southward.

3. Waves beating the reefs into islands.

[1] See Smith, Hilgard, Heilprin, and Dall, for the structure of the peninsula of Florida.

[2] I can hardly see how Leconte states (Nature, October 4, 1880, p. 558) that there are barrier reefs in Florida with lagoons from ten to forty miles wide, though he subsequently (Nature, November 25, 1880) modifies this statement by indicating this to mean the space between the southern coast of Florida and the line of Keys (Old Barrier Reef) which widens from a few miles at its eastern part to more than forty miles in its western part. But this is also misleading, as it refers to the time when the Keys formed the reef, while now the channel between the line of Keys and the present reef gradually widens from a narrow lagoon near Key Biscayne to from six to ten miles wide, opposite the Marquesas, and is about one hundred and fifty miles long.

4. Débris from the reef and Keys on the one side, and the mainland already built (Keys) on the other, filling up the successive channels, and converting them first into swamps and finally into dry land, in all of which he agrees with Agassiz's explanation of the causes which have built the Florida Reef.

Neither was I able, when visiting the Alacran Reef, the reefs of the Windward Islands,[1] the elevated reefs of Barbados, of San Domingo, and of Cuba, the great barrier reef of Cuba, and becoming acquainted with the immense limestone banks so characteristic of the Caribbean region, to satisfy myself that Darwin's theory of subsidence gave an explanation of the condition of things now existing in an area of elevation, and including all the types of reefs which he considered as characteristic of an area of subsidence. If we pass to the Bermudas, Rein,[2] who carefully explored the islands, came to the same conclusion, and took a most decided stand against the theory of subsidence. Rein is of the opinion that coral reefs may grow wherever the conditions of the bottom are favorable for the development of the corals. In these he includes the temperature, the purity of the water, the supply of food by the sea, as well as a solid substructure, whether this substructure be due to the subsidence of the coast, or to an elevation of the bottom, this elevation being caused either by volcanic, organic, or other agency.

Rein also calls attention to the fact, that both Darwin and Dana have assumed a possibility as a fact, and, the theory once given, have attempted to prove the subsidence, instead of bringing the subsidence of coral reefs as a proof of the theory. Proofs of subsidence have nowhere been given except as explanations of existing phenomena, while the proofs of elevations within the regions of coral reefs are innumerable. Darwin and Dana explain the existence of deep channels between barrier reefs and the coast, as well as the formation of atolls by subsidence, and hence conclude from the existence of numerous barrier reefs and atolls that the coasts have sunk, and many islands have been buried in the sea to form atolls. It naturally follows that they calculate the vertical thickness of coral reefs as due to the same cause, and nothing but boring will settle this point.

Rein further mentions a number of coral reefs from the Tertiary to the Jurassic, none of which were more than thirty meters thick. Rein,[3]

[1] Agassiz, A., Three Cruises of the Blake, 1888, Vol. I., "The Florida Reef."

[2] Rein, J. J., Beiträge zur physikalischen Geographie der Bermuda Inseln, Bericht über die Senkenb. Naturf. Gesell., Mai, 1870, p. 140.

[3] Die Bermudas-Inseln und ihre Korallenriffe, nebst einem Nachtrage gegen die

in his excellent sketch of the Bermudas, calls attention to the discovery by Pourtalès of a conglomerate off the Florida reef, (the Pourtalès Plateau,) formed by the remnants of the calcareous remains of numerous invertebrates mixed with coral ooze and sand, which has little by little been built up from great depths. He suggests that the foundation of the Bermudas consists of a submarine bank of a similar nature, which has gradually been built up to the level at which coral reefs can flourish, the Bermuda limestone itself having had its origin upon a mountain or a terrestrial fold, which may consist of rocks having a greater or less geological age. He thus accounts in a most natural manner for the existence of the same rock which forms the surface of the Bermudas at the greatest depths which have been excavated in making the dock at that station. The limestone bank once having been built up to the level at which corals will thrive, the floating embryos carried north by the Gulf Stream found a foothold on which they began to grow, and founded the existing active coral reef. The action of the winds on the beach sand very soon formed the elevated Æolian rocks, which rise to a height of over two hundred and forty feet, and of which he, Thomson,[1] and Moseley[2] have given such excellent accounts. Jukes[3] had already, in 1845, given a similar account of such an Æolian formation at Raines Island, and Dana, in the Geology of the United States Exploring Expedition, had carefully described the formation of the sand drifts solidified into dunes and encrusting layers along the shores of Oahu.

Thomson, on page 304 of "The Atlantic," has given a graphic account of the mode of origin of the Bermudas, when once the weather edge of the reef was raised above the level of the sea, and of the manner in which the Bermudas of the present day have been built up as a bank of blown sand in various stages of consolidation, though Thomson adopts Darwin's theory, that the atoll of the Bermudas is due to the entire disappearance by subsidence of the island round which the reef was originally formed.

Thomson also gives, on page 309, excellent figures of the stratified Æolian rocks of the Bermudas, and of Æolian beds in process of formation, and on the following pages a figure of a so-called sand glacier, or a

Darwin'sche Senkungstheorie. Verhandl. d. ersten Deutschen Geographen Tage zu Berlin im Jahre 1881.

[1] Thomson, Voyage of the Challenger, "The Atlantic," 1877, Vol. I., Bermudas, p. 420.

[2] Moseley, N. H., Notes of a Naturalist.

[3] Jukes, J. B., Voyage of the Fly.

mass of coral sand some twenty-five feet thick, progressing inland. He also describes the mode in which the free coral sand is rapidly cemented into limestone by the action of rain-water containing carbonic acid, which takes up a little of the lime and on evaporating forms the successive crust lines of demarcation between various layers of sand, forming the stratification and lamination of the Æolian rocks. The section given by Thomson, as exposed by the cutting made for the floating dock in 1870, seems to prove a slight subsidence, as there was found a bed of a kind of peat at a depth of forty-seven feet, containing stumps of cedar in a vertical position lying upon the hard bare rock. But it does not prove that this subsidence, or a greater one, which cannot be proved, has been the cause of the atoll shape of the Bermudas, any more than the slight elevations of from twenty to fifty feet, such as we so often meet with in volcanic districts, prove that the special type of coral reefs existing there have been due to their influence.

Lieutenant Nelson [1] has given an account of the geological details of the appearance of the different islands composing the Bermudas, and of the encroachments by the sea and sands, and it did not escape him that the whole of the Bermudas "may be called organic formations, as they present but one mass of animal remains in various stages of comminution and disintegration," and he also called attention to the organic composition of what he calls Bermuda chalk, which corresponds evidently to what has more recently been called coral ooze. He was among the first to notice the important action of Serpulæ in cementing together pieces of coral, and in certain localities forming even small independent reef patches. This has been fully confirmed by other observers in other districts.

Nelson has also suggested the possibility of the formation of submarine mountains by the growth of marine invertebrates round any base they may meet, the decay of their calcareous remains adding stability and bulk to the colony, while around their summits coral reefs would grow. He also says, very truly, "Zoöphytes affect a vertical growth, and in this attitude have a tendency to add to the accumulations of the exterior fence, to the prejudice of the space circumscribed."

When we pass to the very regions explored by Darwin, Mr. Henry O. Forbes,[2] who in 1879 examined the Keeling Atoll, forty-three years after Darwin's visit, — the very one which Darwin first examined, and which suggested to him his whole theory, — could not satisfy himself

[1] Trans. Geol. Soc. of London, V., Part I., 1840, p. 103.

[2] A Naturalist's Wanderings in the Eastern Archipelago, London, 1885.

that there was any proof of subsidence, or that the causes cited by the opponents of Darwin's theory were not amply sufficient to account for all the phenomena he observed there. Mr. Forbes, who spent more than a month in its study, felt inclined to believe that the Keeling Reef foundation has been formed as suggested by Murray, Agassiz, and Semper, and that the islets have been the result of the combined action of storms and the slow elevation of the volcanically upheaved ocean floor on which the reef is built.

Semper,[1] who visited the Pelew Archipelago in 1863, was among the first to come to the conclusion that the presence of barrier reefs, atolls, and fringing reefs in one district could not be explained by the theory of subsidence, and he looked to natural and simpler causes to explain the reefs of the Pelew Islands. He was one of the first, after the general adoption of Darwin's theory of the formation of coral reefs, to visit an atoll district in the Pacific, and he was the first also to point out for that region a condition of things which seemed to him incompatible with the accepted view. He found at the Pelew Islands, within a comparatively restricted area, atolls, barrier reefs, and fringing reefs. He speaks of the channels eaten away between the coast and the barrier reef, distant three to six miles from shore, and forming a labyrinth of channels, which he considers as due to the action of currents, and in which the flow of brackish water prevents the ready growth of corals, while in the case of the barrier reefs less than half a mile or so from the shore the action of the currents is reduced to a minimum and the channels scarcely marked. He speaks of elevated coral reefs of two hundred and fifty feet in height, and comes to the conclusion that the presence of atolls, barrier reefs, and fringing reefs in an area where there had been elevation, and which had remained stationary for a long period, does not indicate that they have been formed during a period of subsidence, while their simultaneous existence would seem to preclude such a conclusion.

Semper is inclined to attribute to the action of currents mainly the great irregularities existing in reefs, which may form even closed atolls, and are in great degree dependent for their ultimate shape upon the configuration of the underlying base. On steep shores barrier reefs, according to him, could not flourish; only fringing reefs closely hugging

[1] Semper, Carl, Die Philippinen und ihre Bewohner, pp. 100–108, Würzburg, 1869. A reprint, with additions, of Semper's article in Zeits. f. Wiss. Zool., XIII. p. 558, 1868. Also, Die Natürlichen Existenzbedingungen der Thiere, Leipzig, 1880, Zweiter Theil, p. 39.

the shores, would thrive in such a position, and he lays great stress also on the difference to be traced in the conditions of the two sides of the same islands, where the one side is exposed to the action of the open sea, while on the other side the long periods of calms are most favorable to the growth of corals. Although Semper does not deny that subsidence may have accompanied in some cases the formation of atolls and of barrier reefs, yet the explanation of the existing conditions of the reefs of the Pelew Islands seems to him more plausible by the theory of currents than by that of subsidence.

Semper has more fully developed these views in his "Natürliche Existenzbedingungen der Thiere." He calls attention to the difference between the theories of Darwin and Dana, while Dana agrees with Darwin that atolls and barrier reefs can only be formed in regions of subsidence, he differs from Darwin in claiming that fringing reefs indicate a greater amount of subsidence than either of the other types of reefs. He looks upon the steep coast line of many volcanic islands as a proof that there has been great subsidence, and of course upon such steep shores, often with a vertical cliff of more than one hundred and fifty feet, there is no possibility of the formation of a fringing reef. We must admit, with Dana, that in the volcanic regions of the Pacific, for which Darwin claims a general subsidence, there have been local phenomena of elevation, and also that in regions of elevation a slight subsidence may also have taken place. But if we have to depend upon either elevation or subsidence to account for the structure of the reefs, there seems to be no possible application of a general law regulating the shape of the reefs. Darwin's map of districts of elevation and of subsidence shows that he considered a region of elevation as one where fringing reefs alone could be formed.

The basis of the whole of Semper's objections lies in the presence of barrier reefs, atolls, and fringing reefs in the same region, and he has attempted to prove that he can explain their presence and peculiar conformation by the action of currents upon growing reefs in a region which has been assumed, according to Darwin's theory, to be one of subsidence. Semper and Rein were among the first to see the importance of the discovery by Pourtalès of the formation of great limestone plateaus at considerable depth, far below that at which corals can grow, and the possibility of having thus many extensive plateaus growing gradually up to the depth at which corals can flourish. The close connection of elevated and growing reefs are strong proofs against subsidence. To establish this view, we are obliged to prove that the peculiar shape of the

different types of coral reefs can be explained by the action of known forces. The moment corals have begun to grow, there is nothing to show that they are not at once subjected practically, though in a less degree, to the same conditions as exist at the surface, since a more or less extensive talus is formed in the sea just as at the sea level. The apparently simple method of continuing the slope of the land into the sea, and thus figuring out the depth of the reef, seems to me a most fallacious one. Let us look at the various sections which are known on our northern coast off the Bahamas, off the coast of Florida, off the Windward Islands, and off the coast of Georgia. These are all of different types, and in a region of coral growth would lead to very different conclusions. The Florida section, which has been given with considerable detail,[1] is perhaps one of the most interesting. The great mass of observations since the promulgation of Darwin's theory is on the side of the more recent explanation of the formation of coral reefs, while the older theory rests upon an hypothesis of which it is under most circumstances extremely difficult to obtain any proof whatever.

Doctor Guppy,[2] who spent considerable time in studying the Solomon Islands, and more particularly the geology and the formation of the calcareous limestones and reefs of the group, altogether dissents from Darwin's explanation of the formation of such a reef as he observed.

Guppy, in his memoir on the calcareous formations of the Solomon Group, has plainly shown that in that group of islands upraised reef masses, whether atoll, barrier reef, or fringing reef, have been formed in a region of elevation, and such upraised reefs are of moderate thickness, their vertical measurement not exceeding the limit of the depth of the coral reef zone, — one hundred and fifty to two hundred feet at the very outside. While this is undoubtedly the case where the reef masses rest upon a foundation of volcanic or older submerged rocks, yet the presence of coral reefs upon foundations of modern limestone, as in the West Indies, made up of fragments of the calcareous remains of all kinds of invertebrates, among which may be deep-sea corals, makes it difficult to fix very accurately the limit of demarcation between the reef limestone proper and other recent limestones when both have been modified and changed in elevated areas into the hard ringing compact limestones so characteristic of all areas of elevation. At the Solomon Islands, the

[1] A. Agassiz, The Tortugas and Florida Reefs, Mem. Am. Acad., 1883.

[2] Guppy, H. B., Suggestions as to the Mode of Formation of Barrier Reefs in Bougainville Straits, Solomon Group, Proc. Lin. Soc. of New South Wales, IX., 1884, p. 949.

presence of foraminiferal limestones of concretions of manganese, up to a height of nearly nine hundred feet, (the limit is usually, according to Guppy, five to six hundred feet,) would indicate a total elevation of more than twelve or fifteen hundred feet, and there appears to be no reason, from what we know of the formation of barrier and of fringing reefs, and of their extension seaward, why the thickness of the reef limestone should be limited to one hundred and fifty or two hundred feet even in an area of elevation.

Guppy infers that corals may begin to build at greater depths than those usually assigned, as some of the elevated reefs in the Solomon Islands "rest upon partially consolidated calcareous ooze, which is not found in depths under fifty fathoms on the outer slope of the present reef; that in the case of reefs with a gradual slope, where the lower margin of the band of detritus lies within the zone of reef-building corals, a line of barrier reefs will be ultimately formed beyond this band, with a deep channel inside; but if the band is formed on a steep slope, and reaches beyond the limit of reef-building corals, no such barrier reef will be found on account of the silt."

It is not necessary, as is supposed by Guppy,[1] in his account of the Coral Reefs of the Solomon Islands, to have an upheaval to bring corals within the constructive power of the breakers. Their natural growth is quite sufficient to raise them beyond that point. He gives for the formation of barrier reefs, and as an explanation of the existence of a lagoon inside of the reef, the same explanation as is given by Leconte, — that the outer growth of the corals is in the direction of clear water, while it is limited inland by the silt and muddy character of the water of the barrier reef channel. He is also inclined to attribute the cause of consecutive barrier reefs to elevation. This certainly has not been the cause in Florida. The reefs have grown up from the bottom wherever the platform had attained the proper level for coral growth.

Bourne, who examined the Diego Garcia atoll[2] and the coral formations of the Indian Ocean, came to the conclusion that the whole character of the Chagos group is very much opposed to the theory that atolls and barrier reefs are formed during subsidence. There are several atolls rising above the waves, that of Peros Banhos being fifty-five miles in circuit, and composed of numerous small islets placed upon a ring-shaped

[1] Guppy, Solomon Islands, Calcareous Formation of the Solomon Group, Proc. R. S. Edinb., XXXII. Part III., 1885.

[2] The Atoll of Diego Garcia and the Coral Formations of the Indian Ocean, by J. C. Bourne, Nature, March 1, 1888, p. 414; April 5, 1888, p 546.

reef, through which there are several large and deep channels. Egmont, or Six Islands, is an instance of an atoll in which the encircling reef is perfect, and unbroken by any channels. There are several submerged banks, nearly all of which have an atoll form. The great Chagos Bank is a huge submerged atoll; so are the Pitts, Ganges, and Centurion banks. Darwin considered that the Great Chagos Bank afforded particularly good evidence of the truth of the subsidence theory, yet Mr. Bourne considers that a more intimate knowledge of the Great Chagos Bank, and of the relations of it and other submerged banks of existing land, shows this view to be untenable. For as the rim of the Great Chagos Bank is on an average only six fathoms below the surface, and in the most favorable depth for growth of corals, there are actually six islets on the north-western edge rising above high water. Bourne has also noticed the great and rapid destruction of parts of Diego Garcia, both inside and outside of the lagoon, and has called attention to the transfer of material due to storms and tides, showing that the normal action of tides and winds and waves is constantly tending to lower the sea level, and thus lay bare dry land that may have been formed by elevation or otherwise. It does not seem surprising, therefore, that the majority of atolls and barrier reefs are under such circumstances only just able to maintain their surfaces above the sea level. He gives an explanation of atollons in the centre of large lagoons, based upon the production of oceanic conditions in the interior of a large lagoon, as in Tilla-dou-Matte, where he thinks the atollons have been formed before any land reached the surface, in which the islets forming the large lagoon were few in number and distant from one another, so that the atollon would practically have an oceanic character, and be swept by currents, establishing all the conditions for a new atoll. The corals thus flourishing on the circumferential parts of the reef surrounding the islet, new atolls with shallow lagoons would be formed as long as the deep channels between the outer distant islets were swept by strong currents, becoming wider and deeper because corals could not thrive in them.

Bourne emphasizes the favorable conditions under which corals flourish as occurring in localities where there is a moderate current flowing over them, not so strong as to dash them to pieces, but strong enough to prevent the deposition of sand, these conditions being found everywhere in external slopes. He lays greater stress on currents than on food supply, as he considers that to be at variance with the existence of thriving coral patches within a lagoon. While we do not deny the fact, yet the lagoon patches do not spread as vigorously as the corals growing on the

exterior of the reef, or else they would soon obliterate all traces of the lagoon. Yet I can hardly see that he has made out a case, that the corals on the outside of a lagoon on the face of a reef, in full exposure to oceanic currents, laden with food, are not infinitely better off, and naturally grow more vigorously, than those which, as in a lagoon, are cut off from a great part of their food supply. They are able to grow in lagoons in spite of this, because they grow in localities which are kept clean. As I have plainly shown in the Tortugas, all corals grow remarkably well on the edge of channels, above the sand drifted by the waves and currents inland.

The following observations on the Coral Reefs of the Sandwich Islands were made in the winter of 1885, and formed the substance of a lecture delivered at Honolulu during my stay there. I have to thank Prof. W. D. Alexander for important assistance during my visit, and for the communication of valuable information from the archives of the Surveyor General's Office. Prof. James D. Dana has given an admirable account of the elevated coral reefs of Oahu, and of the extent of the distribution of reefs on the Hawaiian group. Brigham has also added many interesting observations on the coral reefs of the Sandwich Islands, and Captain Dutton in his exploration of the group noted incidentally some points bearing on the subject. Couthouy has also given a description of the elevated coral reefs of the vicinity of Honolulu, as well as of the elevated beaches of Kauai.[1] My own observations supplement those of Dana. I have gone over very much the same ground he covered in 1843, limiting myself, however, to the examination of the reef area proper, as far as it includes the living and the elevated reefs of the islands which I visited, — Oahu, Maui, and Hawaii. For my knowledge of the reefs on the other islands I am indebted to the observations of Couthouy, Dana, and of Brigham.

All investigators of coral reefs agree that corals grow in greatest perfection in the comparatively still waters of inner channels. Thus, in the Tortugas, the largest masses of Mæandrinas and Astræans are found in the old channels between formerly distinct reefs, while the great coral heads, measuring no less than twelve to fifteen feet in diameter, reach their maximum size in the so-called ship channel between the outer reef of Florida and the line of the Keys. As in Florida, so in the Sandwich Islands, the most luxurious growth of Madrepores occurs upon the face of the inner channels. There are, for instance, huge masses of

[1] Couthouy, Joseph P., Remarks upon Coral Formations in the Pacific, Journal Bost. Soc. Nat. Hist., 1842, p. 146.

a species of Porites on the inner channels opening to the sea on the fringing reef of the south shore of Oahu. In the enclosed harbor of Kaneohe there are numerous examples of hummocks, on the summits of which the corals have died on reaching the surface, while the sides are still covered with magnificent clusters of Pocillopores and Porites. Other hummocks in the same locality, not yet above the surface of the water, remain covered with this luxuriant growth, giving shelter also, wherever sand has accumulated between the single masses, to the simpler Fungiæ so characteristic of the Pacific reefs.

Dana has called attention to the manner in which parts of the surface of the inner reef of Tongatabu has become solidified by the cementing material, sand and small fragments, into a huge pavement exceeding in compactness that of the corals themselves, so that coral rock formed from the filling of the interstices of masses of branching corals may become solid enough to be used for building purposes, as is the case at Honolulu.

The entrance to the harbor of Honolulu (Plates IV., VI.) is nothing but a channel kept open by the flow of the river, which empties to the west of Honolulu from the Nuuanu valley, and has killed the corals in its path, scouring at the same time in freshets the whole harbor and the adjacent limestone walls forming the channel (Plate VII.). This and another channel farther to the westward separate the Pearl River Reef from the Honolulu Reef proper. The river forming the Honolulu harbor brings down a large amount of volcanic mud in its short course, and has deposited this in the harbor and channel, so that there appears to be nothing but dark volcanic mud for a considerable distance out towards the entrance of the channel, where the coral limestone reappears.

A similar channel, but not so well defined, exists opposite the creek forming the drainage of Manoa valley, which empties on to the reef at Waikiki (Plates IV., IX.); but this river does not bring down the amount of volcanic silt and detritus carried by the Nuuanu drainage, as it deposits a great part of its burden along the plain through which it flows before reaching the shore, whereas the river emptying from the Nuuanu has a very steep course until it reaches the harbor (Plate X.).

The Pearl River Lagoon outlet, in its turn, divides the reef again by a deep channel (Plates IV., XI.). The amount of fresh water pouring into the lagoon is much larger than that emptying into the harbor, and some of the deep ravines which drain into it extend nearly half the length of the island toward Waialua. A good part of the western slope of the

East Range also drains into the lagoon. Pearl River Lagoon is the remnant of an old entrance like that of Honolulu, when the old shore line was just inside the great plain of coral rock extending to the westward of the lagoon as far as Kalaeloa, the shore line being then its inner line.

The very characteristic bedded coral sand rock so common along the shores of the Florida Keys and of the Tortugas is not common on the southern reef of the island of Oahu. It is replaced by the formation of the massive coral sandstone pavement described above. This, however, is, as with the finer-grained sandstone, often broken into large rectangular slabs, which in their turn have been uplifted by seas unusually heavy, and thrown back on the more exposed beaches.

A very characteristic formation found only on the shores of volcanic islands fringed with corals is the peculiar pudding-stone formed of rounded and water-worn pebbles of volcanic origin, derived from adjoining basaltic rocks dipping into the sea. These pebbles are cemented together by coral limestone, sometimes only a single stone in a mass of white coral or the cementing material merely filling the interstices and barely holding the pebbles together. So that we have all possible gradations between a compact coral sandstone, with here and there a pebble enclosed, and loose friable and poorly cemented rock. There is no locality on Oahu where the process of formation of this conglomerate can be better seen than at the very eastern extremity of the Honolulu reef, at the foot of Diamond Head. This pudding-stone has already been described by Dana, who also called attention to the fact that some of the pebbles are evenly covered with a very thin incrustation of lime, looking as if they had been dipped in milk. The lime in solution is also frequently deposited in the seams of the volcanic rocks, which then resemble irregular dikes, and their cavities when filled with limestone change cellular lava into a sort of amygdaloid. Perhaps no better evidence of the amount of carbonate of lime taken up by sea-water can be given than that furnished by this constant deposition of lime from evaporation of apparently pure sea-water.

The Sandwich Islands are peculiarly placed in the track of the trade winds, so that they all present a dry and a moist side. One side is rediant with verdure, and its mountain slopes are furrowed by innumerable streams, cutting deep valleys on the weather face. The streams become powerful torrents during the rainy season, and pour an immense amount of fresh water into the sea, — so large a quantity as materially to influence the growth of coral reefs on that side. An examination of the

distribution of coral reefs, and of the streams of the islands of Oahu, Maui, and Hawaii, clearly shows this interdependence (Plate I.), the coral reefs being most prominent on the lee side. Combining with this the effect of the prevailing currents in bringing pelagic food to the growing reefs, we have a most natural explanation for the absence of coral reefs to the leeward of Hawaii, while the influence of the flood of fresh water readily explains their absence along those parts of the shores of Maui, of Oahu, of Hawaii, of Molokai, where they are not indicated on the map. With the exception of a few patches of Pocillopora near Hilo, to the south of the harbor, and on the west face of the island near Kawaihae and Upolu, there are no corals to be found. In fact, we can hardly conceive of a less favorable shore for coral reefs than the east face of Hawaii, where from Hilo north there are in a length of about ninety miles over a hundred water-falls, many falling perpendicularly into the sea from great height, or pouring in rapid torrents down the steep banks and cañons of the eastern shore.[1] Just as little could we expect, and for the same reason, coral reefs to thrive on western Maui. Except at the junction of the two parts of this island, we find nowhere conditions favorable for the growth of coral reefs (Plate III.).

The coral formation of Kauai, which extends as a narrow growing reef on the eastern and windward shore, has been described by Dana. He has also given an account of the solidified beach deposits [2] similar to the drift sand rocks of Oahu, and has figured a solidified beach deposit occurring along the shores of the Koloa district, the remnant of a narrow fringing reef, which seems to run more or less continuously along the whole eastern sea face of the island.

Brigham [3] is of the opinion that the reef near Koolaii (Kauai) has been elevated. He also says [4] that ten or twelve miles west of Waimea the coral reef has been elevated on a long wide ridge transversely to the present shore line. Near Lápa he speaks of a very curious sand-bank, nearly sixty feet in height, formed by the winds and currents.

[1] Dana does not consider that fresh water has a great influence in the formation of harbors in coral areas, but it undoubtedly at low stages of the tide increases the volume of water which scours the harbors, while the detritus it carries must prevent corals from growing along its course, even if the fresh water was not itself a check to the growth of coral. Though corals in many instances are known to live close to fresh water, yet the fact remains that they do not thrive along coasts where large bodies of water empty into the sea.

[2] Dana, U. S. Expl. Expedition, Geol. Report, pp. 275–277.

[3] Brigham, W. T., On the Volcanic Phenomena of the Hawaiian Islands, p. 344, Mem. Bost. Soc. Nat. Hist., I., Part III., 1868.

[4] Ibid., p. 349.

He further says,[1] that the plain land of Niihau, which comprises two thirds of its surface, is composed of coral reef sand, and the detritus washed from the mountains in successive layers. He also says that the coral reef has been elevated from fifty to one hundred feet, and at the southeast end of the island is quite level. This level portion is bare and hard; the coral structure is not evident, its fracture is conchoidal, and it has a metallic ring. Opposite Kaula the reef is covered with sand in round hills, which have a thin crust of earth.

Brigham has noticed that the limits of the coral reefs could readily be traced by the marked change in color of the water of the fringing reefs, which extend to a considerable distance from shore, usually remaining quite level as far as the outer edge, when they drop into deeper water.[2] No detached coral reefs are known in any of the channels between this island. This is very noticeable off Molokai, where there is a fringing reef on the lee side, which can be plainly seen while steaming along its shore. But whether the coral said to have been obtained there by Rev. Mr. Andrew at a height of three or four hundred feet above the level of the sea is drift coral sand, or indicates a corresponding elevation of the island, I am unable to state.

Nowhere do the drift coral sands seem to play such an important part as on the windward side of some of the Sandwich Islands. This is due to their position in the belt of the trade winds, and to the immediate proximity of the fringing reef to the shore. In some cases the sands merely drift with the wind, forming irregular banks, which become cemented together by the action of the rains into a more or less friable sand rock. The sand rock consists of thin distinct layers, indicating the successive duration of the winds which have driven the sand in a given direction; the successive layers are frequently separated by a thin smooth crust, formed by the action of water on the exposed surface. On the weather side of Oahu, all the way from Kahuku Point to Diamond Head, we meet with such sand drifts (Plate II.). Where the hillsides are more exposed to the full force of the trade winds in the range of an old elevated reef which is pounding to pieces, as at Laie, the sands are carried far inland towards Kahuku Point (Plate II.), where they form well weathered pointed pinnacles of disintegrated sand rock, and assume most fantastic shapes, reaching to a height of over two hundred feet above the level of the sea, the material having been furnished by the drift from the disintegration of the old reef; the loose sand is first swept inland by the trades, and banked up in layers, which are subsequently

[1] Ibid., p. 351. [2] Ibid., p. 352.

furrowed and torn by the rain waters, and either cemented or disintegrated into the shape they now present.

Dana has given a figure [1] of one of the best examples of such drift sand rock, which is found near Kahuku Point, at an elevation of about seventy-five feet above the level of the sea. As he states, the island of Oahu has undergone an elevation of somewhat more than twenty feet, since these sandstone bluffs were formed, and this bluff before its elevation undoubtedly occupied the same relation to the fringing reef which now forms the elevated plain back of Kahuku Point as the sandstone rocky bluff of Laie Point holds to the present edge of the shore. Organic remains are very rarely found in these coral sandstones, although an occasional shell left by a hermit crab, or a thin fragment of coral or of a Lamellibranch may sometimes be rolled up into the sand drift and cemented in it. A walk on the long steep coral sea-beach extending from Kahuku Point to Laie shows at once where the material for these coral sandstone bluffs must have come from.

On Maui we also have a long coral sand beach stretching from Kahului Bay to Paia (Plate III.), from which drifts have been blown, forming extensive coral limestone deposits on the base of the eastern slope of Western Maui, near Wailuku. The drifts have in some cases formed large heaps of considerable height, which have accumulated on the mountain sides for nearly the whole length of the line of separation between Eastern and Western Maui. These accumulations of limestone vary in thickness from a few thin layers, scarcely concealing the undulations of the ground beneath and forming a thin veneer, to drifts of considerable magnitude, with rounded tops, more or less disintegrated, and showing plainly in section the successive layers which have formed them. Through the thinner layers frequently crop out the grasses and plants which have been partially covered by the drifting coral sand, while in the thicker deposits the vegetable matter is found in all possible stages of decomposition, finally leaving tubular spaces, which have been attributed to annelids by some observers, and supposed thus to prove a very considerable elevation of certain parts of the Sandwich Islands, as at Wailuku, where Captain Dutton [2] mentions this drift coral sandstone as fragments of an elevated coral reef.

The low plain which separates Eastern and Western Maui (Plate III.), extending from the landing at Maalaea to Kahului Bay, the harbor of Wailuku, on the north, is the top of an old coral reef, which flourished

[1] Geology of U. S. Exploring Expedition, p. 46.

[2] Report of Director of U. S. Geological Survey, 1883, p. 201.

when the inlet still gave free entrance for the sea-water driven through it by the trade winds. The reef finally choked up this passage, flourishing thereafter only at the northern edge, where it is still active. Little by little the old reef has been completely hidden by the mass of drift sand derived from the beach of coral limestone sand to the east of Spreckelsville, which at one time may have been much farther inland. The coral sand on the beach is finely triturated, and the finer fragments form regular dunes of all possible sizes, from small horseshoe-shaped heaps, driven slowly along by the trades and growing constantly, so that we find some of these dunes of no less than twenty feet in height, which have travelled two to three miles towards the foot of the Western Maui slope, where they are comparatively sheltered and become cemented together by the rain. The Spreckelsville beach thus supplies the driftiug coral sand, afterward hardened into the rock mentioned above, as well as the remarkable sand dunes which travel inland, obstructing the roads and the trails. They resemble the huge travelling sand dunes found on the desert back of Mollendo, which frequently cross the railroad tracks leading to Arequipa, and impede the progress of trains as much as snow drifts do in a northern region.

In estimating the thickness of coral reefs,[1] it has been usual to take the declivity of the land, and to calculate from the estimated slope and distance from shore the thickness at any given point. This must be a very defective method, at least in volcanic countries, where the fringing coral reefs have frequently been entirely covered over by volcanic outbursts, such as ashes, lava, or perhaps torrential rains, bringing down from the mountain-sides an unusual amount of detrital matter. The drilling for artesian wells near Honolulu has most plainly shown this alternation of growth of reef corals and of either lava outflows or water-

[1] Darwin and Dana both argue that the subsidence of the land is the only possible cause for the thickness of a fringing or barrier reef, which may be as much as one or two thousand feet. The evidence brought forward by Mr. W. O. Crosby (On the Elevated Coral Reefs of Cuba, Proc. Bost. Soc. Nat. Hist., 1882, p. 124) does not throw any additional light on Darwin's theory of subsidence; it is of the same character as all the statements which prove the subsidence by the existence of coral reefs, and while there may have been coral reefs formed during subsidence, it does not prove that their growth is due to subsidence any more than the presence of elevated reefs proves them to be due to elevation. They grow and must have flourished continuously in periods of both elevation and subsidence, as long as neither the elevation nor the subsidence was more rapid than the rate of growth of corals, and as long as the area in which they were found as elevated reefs was inside of the limits of depth within which we know corals to grow.

washed material. On the other hand, we may have the coral reef forming merely a shell of very moderate thickness, covering the underlying lava rocks. Such is probably the case with the inner reef of the harbor of Kaneohe (Plate V.), where it is easy in the inner harbor to trace all the transitions from lava islets rising high above high-water mark (Mokolii, Plate V.), and surrounded at the base with a thin layer of coral, or to similar islands scarcely reaching above the water level (Ahuo Laka Mokuo Loe, Plate V.), where the lava rock can be seen in the centre of the Pocilleporæ surrounding it, and again from these to numerous similar islands (Plate V.), which, judging from analogy, have a nucleus of lava, but, not reaching to the water level, have become entirely coated with coral. Finally, there are larger islets which are covered by dead corals in the centre, and fringed only by a circle of living corals, while outside of the harbor we have a reef of greater thickness, probably forming a regular fringing reef on the outside of the entrance to Kaneohe Harbor (Plate V.). The flat plain underlying the northern edge of the harbor, having been built up to reach the water level for nearly its whole width, is covered only with occasional patches of living coral in the deeper parts, and with a flourishing growth of corals on the edges adjoining the inner harbor. Near Kahuku Point there are several most interesting cases, showing the thin veneer of coral which must in some instances cover the underlying lava. It is not uncommon to find at a few rods from the shore what may be called coral tables. They are parts of the elevated coral reef, left as pinnacles on the top of a projecting mass of lava, the coral table being at the same level as the adjoining disconnected elevated coral reefs. These coral tables can hardly have been left cemented where they were unless the intervening coral reef has been all washed away, and they should not be confounded with similar unattached blocks upthrown and not necessarily cemented in their natural attitude, such as have been described by Dana. A very fine specimen of such a large unattached coral rock block is seen lying on the reef across the entrance of Kaneohe Harbor.

In estimating the thickness of a fringing coral reef, the following indications, taken from sections of artesian wells bored in the vicinity of Honolulu, will be of interest.

With the exception of Mr. James Campbell's well and the well near Pearl River Lagoon, the artesian wells are at Honolulu or to the eastward and near Diamond Head. To Messrs. Lewes and Cooke I am indebted for data regarding the character of many of the wells. Water was reached at depths ranging from three hundred to six hundred and

twenty feet, and none of the wells were started at a greater height than forty-two feet above high-water mark.

Palace yard artesian well: —

72 ft. of coral rock.
6 ft. of lava.
Then 260 ft. lava to coral, thickness not given.
Then clay.
Then lava to 706 ft.

A second well half a mile inland from the above: —

30 ft. of boulders.
Coral was reached at 200 ft., of a thickness of 30 ft.
Then 250 ft. of clay.

At Waimea, Oahu, 900 ft. was drilled through hard ringing coral rock; then sand and lava were encountered.

Near Pearl River Lagoon, close to the road running above the elevated coral rock plateau to the southeast of the Pearl Lochs, a well passed through 300 to 400 ft. of coral rock.

Another well passed through

100 ft. of soil and boulders.	30 ft. of coral.
100 ft. of coral.	90 ft. of clay.
12 ft. of clay.	28 ft. of sand and boulders.

A well in Thomas Square: —

6 ft. of soil.	60 ft. of clay.
10 ft. of sand.	50 ft. of coral.
200 ft. of coral.	80 ft. of clay.
44 ft. of clay.	50 ft. hard pan.
10 ft. of coral.	

Another well, after a few feet of surface soil, came upon a bed of

38 ft. of coral.	5 ft. of clay.
Then 22 ft. of white sand.	45 ft. of coral.
43 ft. of yellow sand.	30 ft. of clay.
47 ft. of lava.	100 ft. of coral.
110 ft. of coral.	78 ft. of clay and coral mixed.
100 ft. of lava.	28 ft. of clay.
70 ft. of coral.	120 ft. of lava.

The "coral" in these wells was so ground up that it could only be recognized as such from the larger fragments, and the so-called clay was mainly lava detritus finely pulverized.

The well of Mr. James Campbell is thirty feet above high-water mark.

50 ft. of gravel and beach sand.	20 ft. of soapstone.
270 ft. of tufa.	110 ft. of brown clay.
505 ft. of hard coral.	48 ft. blue lava.
75 ft. of brown clay.	10 ft. of black clay.
25 ft. of washed gravel.	18 ft. of clay.
95 ft. of red clay.	249 ft. hard brown rock (lava).
28 ft. of white coral.	

The well of Mr. A. Marques is at the mouth of Manoa Valley, 36.67 feet above high-water mark : —

10 ft. of earth.	30 ft. of clay.
20 ft. of coral.	150 ft. of lava.
40 ft. of lava.	268 ft. of clay, rock, and lava.

That of Mr. Dillingham is 38.72 feet above high water : —

90 ft. of loam.	25 ft. of coral.
40 ft. of coral.	40 ft. of clay.
60 ft. of clay.	300 ft. of lava.

That of Mr. Ward is 13.36 feet above high-water mark : —

15 ft. of loam.	23 ft. of coral.
180 ft. of hard coral.	107 ft. of sand.
4 ft. of clay.	4 ft. of sand.
24 ft. of coral and shells.	4 ft. of lava.
41 ft. of clay.	18 ft. of lava rock.
10 ft. of hard coral.	35 ft. of rock.
109 ft. of clay.	

There are in the Museum at Honolulu pieces of wood, charred or decomposed, brought up from a depth of two hundred and fifty feet from one of the artesian wells. This would merely indicate that the pieces had been washed down from the mountain sides on the then existing slope, and would not necessarily indicate a subsidence. The alternating of so many successive layers of clay and coral and lava indicates, in my opinion, merely the gradual extension seaward of the shore line as fast as lava detritus was washed down or flowed over from successive eruptions, while the growth of the layers of coral indicates the period of rest during which the coral beds were deposited, each in its turn being overwhelmed by a layer of lava or laval detritus, until we reach the existing condition of things. That such a succession of coral growth and lava beds actually took place in the past can safely be

inferred from the borings of the artesian wells, as well as from what we see going on in the harbor of Kaneohe along its shore line, along the shore line at Diamond Head and other parts of the fringing reefs east and west of Honolulu, as well as in certain portions of the islands where coral sand rock is intercalated between beds of lava of greater or less thickness.

The great thickness of the coral rock can be accounted for by the extension seaward of a growing reef, active only within narrow limits near the surface, which is constantly pushing its way seaward upon the talus formed below the living edge. This talus may be of any thickness, and the older the reef, the greater its height would be, as nothing indicates that in the Hawaiian district there has been any subsidence to account for such a thickness of coral rock in its fringing reef.

Dana thinks that the western coral islands beyond Bird Island, in the Hawaiian range, indicate participation in the general subsidence, which he traces over a large part of the Pacific Ocean, as indicated by atolls and barrier reefs. Yet he himself describes the fringing reefs of Kaui and Oahu, and mentions their width as being considerable.

There appears to be no evidence that there has been any considerable elevation in the Hawaiian Islands, twenty to twenty-five feet being probably the extreme ; while the existence of cinder cones with their base close to the present sea level would indicate also that there had been no special subsidence. There is, however, some evidence of subsidence on the southern shore of Hawaii. At Kalapanu is a sunken plain about a mile wide and two miles long, where there has evidently been a subsidence of about fifty feet ; and the raised coral reef extending along a part of the shore would indicate another change of level in former times. Brigham has given a sketch plan of the plain in Fig. 27, on page 373 of his "Notes on the Volcanoes of the Hawaiian Islands."[1] Plate XIII. shows the position of the sunken beach at Kaimu.

From the recent examination of the islands of the Hawaiian group, and the explanations given by Dutton of the causes determining their present physiognomy, it would be more natural to suppose that the gradual building up of the various islands by overflows and eruptions had overwhelmed such reefs as existed (if any did exist) during the period of great volcanic activity of the islands. There have been as yet no sunken reefs discovered in any of the channels between the islands, and as far as we know the reefs are all littoral formations of the present shore lines.

The greatest depth in the channel between Oahu and Molokai is 317

[1] Mem. Bost. Nat. Hist. Soc., Vol. I. Part III.

fathoms; between Molokai and Maui, 137 fathoms; and between East Maui and Kahoolawe, only 40 to 50 fathoms; while between Maui and Hawaii there is a depth of 1107 fathoms, and over 1890 fathoms close to Kaui between Kaui and Oahu. These soundings were kindly given me by Hon. H. A. Wiedemann, and were taken by a vessel sounding for a submarine cable to communicate between the islands.

It is interesting to note the structure of the reef as we pass over it at high tide from the shore to the sea face. The slope of the channel forming the harbor entrance is made by a steep bank of muddy whitish ooze. The reef-flat itself, varying from half a mile in width to less, is also covered nearer shore with coral ooze, and interrupted by small rounded knobs of decomposed algæ, Nullipores, and stalks of dead Sargassum. These cover irregular patches of greater or less size, separated by bare spaces of ooze. A little farther out, in depths varying from five to six or even ten feet of water, we come across numerous rounded patches, covered by clusters of Millepora, with here and there a group of Pocillopora, and in the intervening bare patches the coral limestone is frequently pitted by numerous Echinometradæ and Diadematidæ. Some of the rounded knolls rise close to the surface, and sometimes even are bare, leaving deep pools between them, in which the characteristic reef fauna flourishes. Such knolls, when farther out to sea, and arranged, as they often are, in regular lines of considerable length parallel in a general way to the trend of the shore, form successive concentric lines of breakers, diminishing towards the shore. Upon these the sea beats, breaking up, pounding to pieces, and triturating the corals growing upon the sides of the knolls, until they are changed into the ooze which gradually cements the shore portions of the reef into a solid limestone mass (see Plate VIII.), and freely supplies the fine material for the coral sand beaches close to the land. On Plate VI. the lines of breakers on the sea face of the reef are faintly indicated. On smooth days I could follow beyond the outer line of the breakers the occasional patches of large Millepores, or of Pocillopora, or Porites, or Astræa, together with the few Gorgoniæ which run out on the somewhat steeper outer slope of the reef. These gradually diminish, and as far as could be seen with the sea glass disappeared completely in about ten fathoms. It was very easy to examine the Honolulu portion of the reef by accompanying the fishermen, who are in the habit of going out daily in their canoes just outside of the breakers, and whose skill in crossing the swell in their outriggered canoes it is very interesting to watch. The small amount of animal life on the Honolulu reef (on the lee side of the island of Oahu) is surprising, as

compared with that on the weather side on the reefs of Kaneohe Bay. This difference is due to the fact that much of the pelagic life brought by the trade winds against the weather side of Oahu is swept past the lee side without bringing any great quantity of food to the coral reef. This is plainly shown by the comparative scarcity of pelagic life, even on the most favorable days, on the lee side along the sea face of the Honolulu reef, as contrasted with that of Kaneohe Bay. On such days little could be seen off Honolulu beyond a few Salpæ, a huge species of Appendicularia in its house, a few Diphyes and Praya, and a few pelagic crustacea, even when the wind had been blowing from the south, and was driving the pelagic fauna towards the lee shores again. The Honolulu reef contrasts also with the Florida Reef in the scarcity of Sponges. The very gradual sea slope of the Honolulu reef is one of its marked characteristics.

The in-shore flat of the reef, left bare at low tide, as well as all the low land extending to the base of the hill slopes to a height of nearly twenty feet above the level of the sea, is made up of coral reef sand. This is the character of the whole reef, whether west of Honolulu or east, all the way from the outskirts of the city to Waikiki, and to the base of Diamond Head. At Diamond Head the coral reef sand is mixed with the volcanic material washed down from its slopes, and where it is washed directly into the sea we find the lava sand as well as the coral sand remodelled by the action of the water, forming either layers of clear lava sand overlaid by coral sand, or all possible gradations between a mixture of fine sands of the two and a modern conglomerate or breccia of the larger fragments cemented together by the lime carbonate held in suspension, or by the finer or coarser sands. Pot-holes, gullies, and corrugations, due to the wearing action of the sea-worn lava gravel rolling up and down the lava beds, characterized them wherever exposed to the action of the breakers or of the sea; while, if subsequently protected, these or similar holes and corrugated surfaces are gradually filled by a deposit of finer or coarser washed material, which, becoming cemented, produces very striking effects. Some of the larger pot-holes in the lava beds in the adjoining elevated portions of the reef often contain masses of Porites and of Mæandria of considerable size, more or less washed, as well as numerous fragments of mollusks, the whole cemented together in a solid calcareous mass, as we find it on the exposed part of the shore edge of the reef. Towards Diamond Head the outer slope of the reef approaches the shore. (Plate IV.) The reef there is narrow, and, owing to the greater depth off shore and the narrowness of

the reef, there are only one or two lines of breakers acting directly upon the shore portion of the reef.

Dana has described the so-called modern chalk of Oahu, which is found at a single locality near Diamond Head, in a part of the elevated coral reef. It is at the foot of a tufa cone rising from the water's edge, and, as Dana has already stated, coral must have been thriving on the shores when the eruption took place, as there are fragments imbedded in the tufa, although the chalk itself is of later origin. There is nothing to be observed throwing any light on the causes which have produced this chalk at this particular part of the elevated reef, except that it must have been deposited in a confined area, subject to special conditions. Yet this chalk is not more similar to the modern chalk than the modern chalk dredged off Nuevitas, which was deposited under most dissimilar circumstances. The Oahu chalk appears to differ very slightly from such deposits of fine coral sand as are deposited in sheltered localities on the shores of coral beaches. It does not contain any organic remains, but has in addition the peculiar fracture of chalk, and, as is stated by Dana, is used on the blackboard in some of the schools of the islands.

At Makapun the reef has been raised about twenty feet, and farther north the whole coast is fringed with a growing reef, extending in some places over three quarters of a mile in width. There are extensive sand dunes, also, mentioned by Dana and Brigham, a short distance back of the shore reef at the foot of Konahuanui.

The elevated reefs of the Sandwich Islands, although not elevated more than twenty to twenty-five feet, are extensively quarried as limestone for building purposes, especially those parts of the reef which evidently formed its inner portion, and in which the corals and mollusks living on the surface of the reef have been admirably preserved.

On the southern edge of the Aliapaakai basin, six miles west of Honolulu and three quarters of a mile from the sea, there is a raised coral reef which has been much displaced; it has been fully described by Dana. Living corals are comparatively rare upon the reef-flat. Large specimens of Porites[1] flourish in pits and hollows of the reef, and a scanty marine fauna, with occasional masses of Nullipores and Sargassum. The top of the edge of the reef is barren, and is deeply furrowed; it is only somewhat farther down the slope that the reef fauna flourishes actively again.

[1] Dana speaks of the huge size of individual masses of Porites in the rock of the inner reef of Tongatabu, which were twenty-five feet in diameter. Geology of U. S. Exploring Expedition, 1849, p 39.

One cannot fail to be struck with the hardiness of the large masses of Porites still found living, half exposed to the air at low tide, in the impurer water of the reef near to the shore, which seem to die more from the effect of sediment than from the effect of the exposure to the sun, or from the impurity of the water. In fact, Porites both at the Sandwich Islands and at the Tortugas are among the hardiest of reef corals. As Jukes, Guppy, and others have noticed, in many species of corals exposure to air is not always fatal, although in Florida the Madrepores, which hold to the Atlantic reefs the same relation the Pocilloporæ hold to the Pacific, are frequently killed over extensive tracts when exposed to air by low tides or winds. As far as I could judge from an examination of the sea face of the Sandwich Island reefs, the Pocilloporæ do not extend to a depth of more than fifteen fathoms, and then gradually disappear, though the sea face of the reef was swept by a constant current running westerly, due to the trade winds, and during the season of trade winds but little sediment found its way there to prevent their active growth.

Dana has called attention to the great extent of the elevated reef of Oahu, which occurs at the foot of the mountain slopes along the whole southern face, at heights ranging from five to twenty feet above the level of the sea, forming the large flats of the Pearl River Lagoon. It is nearly continuous from Makapuu to Kahuku Point, extending from there to a small river emptying at Waimea, where it abruptly ceases, but flourishes again on both sides of Waialua, and along the greater part of the northwestern coast near Waianae. The elevated reef attains its greatest width near Kahuku Point, where it is nearly a mile wide, and we can trace this elevated reef as a fringing reef before the elevation of Oahu just as plainly as we now trace the present fringing reef of the south shore of Oahu, and that in Kaneohe Bay.

Near Kahuku the drift sand-hills are of great size and height, and resemble an elevated beach. The elevated reef near Kahuku and that along the northwest end of Oahu are quite distinct from the solidified sand-dune deposits.

At Laie[1] the drift sand has formed hills of sandstone hard enough for building purposes. These hills are thirty to forty feet high, much broken and worn by the action of rain and wind into grotesque honeycombed masses and ragged pinnacles, which, as Brigham says, have often been mistaken for elevated coral reef rock.

The mouth of the stream at Waimea is often completely closed by a

[1] Brigham, Mem. Bost Soc. Nat. Hist., Vol. I. p. 358.

dam of sand at low stages of water, which is in its turn broken through again whenever sufficient head of water has accumulated behind it.

Some extensive ancient dunes, from one hundred to one hundred and twenty feet in height, indicate an effect of the trade winds now no longer acting. It may be that some of these more ancient inland dunes, which have become solidified near Diamond Head, were formed under the influence of the trades before their full force on the eastern edge of the reef was destroyed by the elevation of the long hill forming Diamond Head. It may be that we owe to the presence of these dunes most of the coral sand and calcareous material which we find up to a considerable elevation between Diamond Head and Honolulu in the Manoa Valley.

Although the Honolulu reef has a far less rich fauna than the reef of Kahului Bay, yet the limestone which it forms, not having been exposed to the action of the trade-wind surf, presents the reef much as we see it, flourishing and gradually dying out in proportion to its proximity to the shore. The corals, Serpulæ, Nullipores, echinoderms, mollusks, and even crustacea, are not ground to pieces, as in reefs open to the violent action of the sea, where all traces of their identity are destroyed in the process of formation of the coral limestones characteristic of such exposed reef shores. On the contrary, the coral heads themselves, as well as all the animals flourishing upon such a protected reef as that of Honolulu, are rapidly fossilified and imbedded in limestone, being gradually covered with the floating lime held in suspension or in solution in the water; so that, whenever we get a good section of the shore coral limestone, we invariably find, either on the reef-flat itself, or on the immediate shore line, or on those portions of the reef which have been slightly elevated, a limestone representing the reef as it grew and flourished, in which we can plainly distinguish the different species of coral, as well as the invertebrates which once lived in their shelter.

In the section to be seen on King Street, near the Prison Point, beyond the bridge, a face of about six feet in height was being quarried, the highest point perhaps three feet above high-water mark, the Prison Knoll, which is the continuation of this limestone ridge, being about ten feet above high-water mark. This and another limestone knoll facing the opening of the Nuuanu Valley are formed of a close white limestone mass of decomposed reef rock, in which the individual heads are more or less distinct, and which contains a large number of shells and echinoderms imbedded in the mass cementing the corals together. The western and eastern extensions of this old shore line of the reef, which must have been elevated about twenty feet above the sea level, has been

preserved; but in the continuation of the dividing ridge between the valleys of Nuuanu and of the Manoa, they have been denuded on each side of that ridge and appear again on the eastward at a few points on Diamond Head and towards it on the west. But the lower levels of the same reef can be traced continuously along the present southern shore line all the way from Diamond Head. The salt ponds and flats, which extend inland in the Manoa Valley between Honolulu and Waikiki seem to indicate an inner lagoon much like that of Pearl River, which has gradually been filled up by the silt swept down by the river.

The comparative poverty of the fauna of the Honolulu reef is undoubtedly due to its being on the lee side of the island of Oahu, the outer face of the reef alone obtaining a fair supply of food, brought by the westerly current due to the trades, which runs along the south coast of Oahu.

Mr. Rose was kind enough to take me out in a canoe to examine the corals in Kaneohe Bay. We found the bottom of the bay covered in many places by numerous more or less circular patches of living corals (Plate V.) in all stages of growth, from domes a few feet below the level of the sea covered by flourishing corals to small fringing reefs round the shores of the islets and rocks which occur in the bay, and to elliptical reefs, awash when the corals were living only on the outer slopes. The bases of all these islands are undoubtedly summits of volcanic rocks projecting above the general level of the bay, which have been coated or surrounded by corals. To the southward of Kaneohe Head, on the plain of Kailua, are extensive dunes similar to those already described.

The edge of the bay is itself entirely surrounded by a fringing reef (Plate V.) of corals, mainly of species of Porites, which have gradually died out near the shore, and thrive only near the deeper water on the edge of the channel. The opening of the bay is barred between Kapapa and Ahuo Laka by a barrier reef (Plate V.) of very moderate thickness, extending towards Kekepa and Mokolii, resting upon a lava bottom, which is exposed in places. There are two entrances into the inner lagoon of the bay. The breakers pound heavily upon this barrier, and from it huge coral blocks are constantly thrown up and ground to pieces, the sand being carried in towards the bay and forming the bar of the harbor. Dana looks upon these huge blocks, as well as the islands off Kaneohe Bay, as having been elevated from six to eight feet above high tide.[1] Kaneohe Bay is to a certain extent sheltered from the full force of the trade winds by the small peninsula of elevated coral reef which stretches to the eastward of the bay. On the barrier reef, as well as on

[1] Dana, J. D., Geology of U. S. Exploring Expedition, p. 253.

the isolated patches in the bay, we find mainly Pocilloporæ, and sheltered by them in the interior circle of the coral patches solitary Fungiæ with a few Gorgoniæ, which seem to be much less numerous than upon the reef near Honolulu, and there are also comparatively few algæ and corallines. The large masses of Porites growing near the shore have little by little been choked by the silt coming down from the Pali, and a volcanic sand flat, with a band of living corals on the outer edge, is thus formed near the fringing reef, in marked contrast to the coral sand flats formed by the action of the breakers.

The whole bay before corals began to flourish upon it must have contained a number of small volcanic islands, and a large number of sunken volcanic rocks and ledges, which have become capped with coral or surrounded by diminutive fringing reefs. What is now going on in the Bay of Kaneohe on a diminutive scale, we may apply to groups of volcanic islands in the Pacific. If we add to this the powerful agency of accumulations of limestone on the deeper summits or banks, until these surfaces are built up to a height at which corals can begin to grow, we have all the various elements needed for the formation of fringing reefs, barrier reefs, or atolls within a comparatively limited area, as is the case in those archipelagoes of the Pacific where these various kinds of reefs have been observed to occur together. The base upon which the barrier reef of Kaneohe has been built up has probably been formed by the washing down and disintegrating of a lava crest of considerable height, if we may judge of it from Mokolii.

According to Dana and Darwin the line of barrier reefs and of atolls indicates the former extent of the area of land before the reefs began to form, which in some cases was three or four times that now above the level of the sea, and in the whole Pacific reef district the atolls and reefs are the monuments of islands which have long ceased to exist.

The formation of a barrier reef upon a foundation denuded to the depth at which corals can flourish has not been observed before. Captain Wharton [1] gives a very interesting account of "the preparation of a suitable foundation for coral builders by a process directly the reverse of that of building up by marine organisms on mounds that have failed to reach the surface," from which it appears probable "that the cinders and ashes which formed, and still form, the summit of the volcanic mound originally thrown up, are being by wave action gradually swept away, and will continue to be so removed until the top of the bank is reduced below the limit of such action, or the solid rock is laid bare."

[1] W. J. L. Wharton, "Foundation of Coral Reefs," Nature, October 11, 1888.

Dana argues against the possibility of coral reefs being planted upon submarine banks of the requisite depths for corals to thrive, yet this is actually what we see going on in Florida, and we can there trace all the steps from the barrier reef to the keys, and to the incipient reef or coral bank making a beginning upon the limestone bank which has been raised by accretion to the depth requisite for the growth of corals. It seems to me that a wide flat reef cannot be formed by a slow subsidence, but must have grown, during a period of rest or slow elevation, simply by the dying out of the coral next to the land, as has been observed on the shore edge of Kaneohe Bay.

Captain Wharton[1] has also given, in a recent number of "Nature," a number of instances of the growth of corals on banks, or on the edge of banks, illustrating the formation of barrier reefs and of atolls without the introduction of subsidence. He instances many cases in which reefs now growing will when awash form perfect atolls of large size, enclosing deep lagoons, without any further deepening by solution. He also calls attention to the great width of many of the existing fringing reefs, which should show more signs of solution than they do if Murray's theory is sufficient to account for the formation of the whole intervening lagoon. The rotten state of the surface of all coral reefs, especially fringing reefs, shows that there is considerable solution as well as removal of material going on; but the very fact that the majority of these reefs are of great width goes to show also that solution alone is not active enough to remove great masses and form lagoons. The case of Rodriguez is cited by Captain Wharton, where, although there is a rise of tide of nearly six feet, with every facility for a scouring action and rapid change of water, yet there is a fringing reef of a width of nearly four miles and three quarters, intersected only by narrow shallow channels. In the case of the Florida Reef there is nothing to show that the outside reef has not arisen on the southern edge of the Florida Reef plateau, when it attained a depth at which corals can grow. The lagoon between the reef and the keys was certainly never filled by corals which have been carried away by solution, though it has been occasionally obstructed by the growth of patches of corals, which are of the same date or of a later growth than the coral reef proper.

Dr. Coppinger[2] describes Amirante Bank as a submerged atoll, which,

[1] "Coral Formations," Nature, February 23, 1888, p. 393.

[2] Cruise of the Alert, by R. W. Coppinger, London, 1882, p. 225. In Florida there is nothing to show that detached barrier reefs cannot grow up to reach the constructive power of breakers, as Guppy seems to argue from the existence of sunken barrier reefs.

if raised fourteen feet, would become a true atoll. According to Guppy,[1] elevation is necessary to form an atoll and bring it within the destructive range of the sea, and a fringing reef, according to him, could not be formed near shore or grow outwards. No such elevating action exists along the whole line of the Florida Keys, yet the reef has grown up to the action of the breakers. The same is the case with Kaneohe Bay.

Neither fringing reefs, nor barrier reefs, nor atolls, grow exclusively outward. I am inclined to consider the islets on the inner side of a lagoon as remnants of islands formed by coral heads and coral sand flats, rather than to suppose that the intervening channel has been eaten away solely by the solvent action of sea-water. Leconte, as I have stated, ascribes the limitation of corals towards the shore, and their growth seaward, on the one hand to the muddiness of the inner waters of the lagoon, and on the other to the purity of the water due to its depth. It really seems doubtful whether the islands in the lagoon channel at Tahiti, mentioned by Murray,[2] are portions of the original reef still left standing, and not, as is the case with the coral heads in the ship channel of the Florida Reef, independent coral patches, which have not been overwhelmed by the action of sediment from the outer reef, or as in the Tortugas, where we find active coral growth in the inner line of the open channels. He further says, when coral reefs are much broken up the coral growths in the lagoon are relatively abundant, while there are but few coral patches and heads in the lagoons and lagoon channels when the reefs rise to the surface, or are nearly continuous. This is certainly the case at Kaneohe Bay.

Geikie[3] also calls attention, in the examination of maps of coral regions, to the difficulty of the theory of subsidence, as in the case of the Fiji Islands, where fringing and barrier reefs and atolls all occur in close proximity, and where all evidence seems to point to elevation, or at least to a long period of rest.

The fringing reef of Kaneohe Bay forms a scalloped outline, with an occasional white coral sand beach where the wind has a wider sweep than in the eastern and more protected parts of the bay. But these

[1] Guppy, H. B., Notes on the Characters and Mode of Formation of the Coral Reefs of the Solomon Islands, being the Results of Observations made in 1882–84, during the Surveying Cruise of H. M. S. Lark. Proc. Royal Soc. Edinb., 1885–86, p. 857.

[2] Murray, Proc. Royal Soc. Edinb., 1879–80, p. 515, April 5, 1880, Vol. X. No. 107.

[3] Geikie, The Origin of Coral Reefs. An Address read before the Royal Physical Society of Edinburgh. Proceedings, Vol. VIII. p. 1, 1884.

coral beaches alternate with darker lava silt brought down from the neighboring mountains, often forming very extensive shore flats, of which the Chinamen, by damming out the sea, have taken advantage for cultivation; along part of Kaneohe Bay there is quite an extensive flat thoroughly cultivated, where cattle are turned out. This flat is formed of coral sand, extending far out to Mokolii Island from the adjoining headland, from which diverge coral patches. On rounding the northern end of the bay we see that the reef north of Mokolii comes close to the shore, and assumes the character of a narrow fringing reef, following the shore line more or less regularly. At Kahana a small harbor has been formed by the extension northward of the reef from Makuua. Westward the road along the edge of the island runs behind the shore sand dunes or the beach shelf, or on its summit. There is no trace of elevation from the point to the south of Kaneohe Bay to the great Kohuku reef-flat, extending south to Laie.

At Kohuku there is a fine bluff of consolidated drift sand, of which Dana has given an excellent figure. Similar drift rocks extend all round the base of the slope of the foot-hills, marking the old shore line of the Kohuku reef, which extends from this point as a flat coral plain, slightly elevated (twenty to twenty-five feet) above the level of the sea, from half a mile to a mile in width, to the present coral sand beach of Kohuku, which is exposed to the full action of the trade-wind breakers, and has thrown up a high sand-bank built up from the elevated reef. This elevated reef extends all the way from Laie to Kohuku, the small outlying islands being the remnants of sand drift rocks which are gradually being eroded by the sea, and which have in former times, when the reef was active, supplied the material for the innumerable sand drifts of the foot-hills. These sand drifts have become gradually eroded into the most fantastic shapes, covering the hillsides with innumerable small points resembling Gothic spires. This elevated reef does not seem to be active on its sea face. No soundings are available for that part of the shore, and the heavy rollers break directly on the present sand beach, so that the sea face is probably quite steep.

Near Waimea the fringing coral reef crops out here and there behind the high sand beach formed from the disintegration of the underlying elevated reef. There, as at Kohuku, the reef seems to stop abruptly near the line of beach breakers, and the slope appears steep, there being no trace of recent reef corals beyond the line of shore breakers. The coral sand at the back of the beach was thrown up to a height of from ten to twenty feet. The breakers form a small lake across a gulch, of which

they dam the outlet by throwing up a high sand dam; this breaks through when the water has accumulated a sufficient head. Half a mile beyond Waimea the coral caps the lava beds at a height of nearly ten feet above the high-water mark.

At one other point two miles beyond Waimea, towards Waialua, we find numerous coral tables capping lava bases. Many of these coral tables are blocks ten by twenty feet, one of them as much as fifty by one hundred feet. The height of the lava supports is usually five or six feet. This elevated coral reef, all the way from Kohuku to Waialua, is cut by lava spits, which project beyond its surface and extend seaward. At Waialua there is a very fine patch of the elevated coral reef, from five to six feet above the level of the sea. Traces of this reef can be seen for five or six miles to the southward of Waialua, along the beach, made up of coral sand mixed with more or less lava sand, which reaches towards Kaena Point.

As will be seen on examining Plate I., the reefs of Hawaii consist only of isolated patches of limited extent near Hilo. On the sides of Upolu Point, both east and west, isolated patches have been observed, near Kawaihae, and at the southernmost point of Hawaii somewhat larger stretches of coral exist.

The so-called coral reef to the south of Hilo (Plate I.), near Keokea Point, consists mainly of detached patches of corals (Pocillopora). They are very much like the patches of corals to be found on the west coast of Mexico, and do not constitute a regular reef, although a good deal of coral grows in this way, judging from the amount of coral sand and fragments thrown upon the small beaches to the south of Hilo. The patches are mainly the same species of Porites and Pocillopora which form the reef of Honolulu. There is comparatively little animal life on these coral patches, and the lava rocks off Hilo do not appear to support a rich fauna. Although small algæ grow thickly on the rocks, no Sargassum was found attached, as near Waikiki on the Honolulu reef, and on the coral conglomerate of the Spreckelsville beach on the north shore of Maui.

Near the northern extremity of Hawaii, near Honoipu, there is a patch of coral and another patch to the eastward of Mahukona, clearly seen from the railroad running round the northern point of Hawaii. On the lee side of Hawaii there is, near the village of Kawaihae, a stretch of coral reef, which protects a bay once a great resort of whalers. The village itself is prettily situated at the northern end of a long coral sand beach. To the south extend, as far as the eye can reach, the

various ancient flows of lava which have come down the slopes of Hualalai and of Mauna Loa; while to the eastward of Kawaihae are seen the older flows of Mauna Kea and the deeply furrowed cañons extending from the shore nearly to the summits of the Kohala mountains. An interesting patch of elevated coral is also found on the edge of the sunken plain of Kalapana, similar to the restricted patches now growing on some points of Hawaii.

The coral reefs of Maui see (Plate III.) are found on the long beach of the windward side of the island, on Maalaea Bay, and along the lee side of Western Maui from Maalaea Bay to a short distance north of Lahaina. The evidence I have been able to collect on the coral plain between Maalaea Bay and Kahului indicates that Eastern and Western Maui have been united by a coral reef, which flourished in the shallow passage once existing between these two parts of Maui. The great coral plain lying at the foot of Western Maui, and extending to meet the slopes of Haleakala on the opposite side, is only the surface of the old coral reefs which once flourished there. The plain which divides the two parts of Maui is in some places scarcely above the level of the sea; it abuts somewhat abruptly on the steep slopes of West Maui, while it passes imperceptibly into the slopes of East Maui at Haleakala.

The corals mentioned by the Rev. Mr. Andrews, as found at elevations of from five hundred to eight hundred feet even on the eastern slopes of West Maui, are, as I have satisfied myself, all Æolian formations such as I have described.

The large reservoir for the Hawaiian Commercial Company, below Wailuku, from one hundred and twenty-five to one hundred and seventy-five feet above the level of the sea, is built in natural depressions left between the sand dunes which have been formed in former times on the old beaches extending all the way across to Maalaea Bay from Kahului Bay. The highest of these sand dunes must be from two hundred to two hundred and fifty feet above the level of the sea, and they have become solidified into sandstones by the action of the rain. Coral sand dunes can now be seen travelling across the road leading from Spreckelsville to Wailuku, some of which are from twenty-five to seventy feet high. But a great many have become fixed at a distance from the beach from which they originated, having become overgrown by a species of Bermuda grass.

Brigham says that on the windward shore of Maui[1] the coral sand is piled up in ridges nearly one hundred feet above the sea, shifting with

[1] Mem. Bost. Soc. Nat. Hist., Vol. I. p 367.

the wind, which sometimes drives columns of sand miles along the beach. This is the material which forms the fine coral sand beach reaching from Wailuku to Paia.

The stratified coral sand rock seen by Captain Dutton[1] at Diamond Head, and to the east of the village of Wailuku on Maui, which he takes as evidence of a recent upheaval of two hundred feet, and perhaps more, are only consolidated sand drifts, such as I have described above. There certainly is nothing in the character of this æolian coral limestone to compare with the consolidated reef rock at the level of the sea. The shells he mentioned as imbedded in it have either been blown up by the violent winter gales, or are the shells of gastropods carried up by hermit crabs, which I have often met with more than a mile from the coast in their wanderings.

I have not seen on the shores of Maui coral ledges indicating any elevation. The highest masses of coral rock are fully within the reach of the action of moderate, or even very heavy seas. The observations of Rev. Mr. Andrews, quoted by Dana, in regard to the possible elevation of Molokai and Maui, do not appear to me to indicate anything beyond coral sand dunes.

The existence of coral sandstone on the east slope of West Maui at a considerable height, over extensive tracts, does not indicate any elevation, but is due merely to the æolian deposits which have found their way to certain favorably situated places under the action of the prevailing trade winds. Nowhere in the district I have examined on Maui have I succeeded in finding any trace of corals beyond the height to which fragments might be carried by the action of the waves or wind and tides of unusually severe storms. The bedding of the sandstones at considerable heights was evidently entirely due, as has been shown by Dana, to the successive deposits of sand cemented together by interrupted rain fall, forming the delicate crusts which separate the various thin layers of coral sandstone which have accumulated at certain points.

I was greatly interested, on visiting the long coral sand beach which extends from Kahului to Hamakuapoko, to find very much the same action going on in the formation of coral conglomerate, breccia, and oölite, which I had so often watched at Loggerhead Key, and on the island of Key West on the beach north of Fort Taylor. This action was, however, modified by the fact that a much heavier sea, due to the trade winds, was driving upon the surface of the reef off the beach, and was still pow-

[1] Hawaiian Volcanoes, by Capt. Clarence Edward Dutton. Fourth Annual Report of U. S. Geological Survey, 1882–83. Washington, 1884, p. 81.

erful enough on the beach itself to throw up huge masses of Porites, of Pocillopora, and of Astræans, and with them a large number of shells living on the reef. The whole is pounded by the process into a sort of coquina, which is cemented on the beach, much like coral breccia. Owing to the steady action of the trades, the finer sands accumulated on the beach would be blown up the slope and carried off to form the travelling dunes, or the masses of drifting coral sand carried inland to form the coral sand drifts, while quite heavy fragments were also blown up bodily to the upper level of the beach.

Kahului Bay is sheltered by a wide, flat, active coral reef, the harbor being an inlet of the western and widest end of the reef. The reef extends easterly, gradually becoming narrower toward Paia, where it ends. Only occasional patches of corals are found to the eastward of this point. It is this extensive coral flat, covered with huge masses of Porites and Pocillopores, upon which the full force of the trade-wind sea is pounding, which furnish many of the larger blocks of the Maui coral coquina which were left as formed in sheltered places, and were covered by a luxuriant growth of a species of Sargassum; the surface of many of these blocks was protected by masses of Nullipores and other calcareous algæ. The Kahului beach is broken by numerous spits extending out on the reef. These spits are remains of lava flows which have become covered with huge rounded masses of lava, and in part by fragments of broken coral and by coral sand, sometimes one to two feet in thickness. In this breccia and conglomerate, as well as in the stratified coral coquina formed in its proximity, numerous rounded and water-worn pebbles of lava have become imbedded. The coral lava conglomerate thus formed has a most striking appearance. I had been greatly puzzled by finding similar deposits inland near Maalaea Bay, on the low plain extending towards Kahului, and on some of the sugar plantations at a distance to the east from the road connecting the above-named places.

The recent British Admiralty Chart, No. 1520, shows very well the distribution of the coral reefs of the Sandwich Islands. The only islands which I examined for reefs myself are Oahu, Maui, and Hawaii, and in passing close to the south shore of Molokai I could readily see from the color of the water that there was an extensive fringing coral reef.

Cambridge, November, 1888.

EXPLANATION OF THE PLATES.

PLATE I.

The Hawaiian Islands. From British Admiralty Chart. Soundings in fathoms. The shaded shore plateaus show the position of coral reefs.

PLATE II.

Oahu. From Hawaiian Government Survey, W. D. Alexander, Surveyor-General. The shaded shore plateau indicates the recent and ancient coral reefs.

PLATE III.

Maui. From Hawaiian Government Survey, W. D. Alexander, Surveyor-General. The shaded shore plateau indicates the position of coral reefs.

PLATE IV.

The south side of Oahu. The shaded portions indicate the position of the active reefs, extending along the south side of Oahu from Barber's Point towards Makapuu Point, and in Kaneohe Bay. From British Admiralty Chart.

PLATE V.

Kaneohe Bay. From Hawaiian Government Survey, W D. Alexander, Surveyor-General. The lined and colored parts indicate the extent of the active reefs of Kaneohe Bay. Soundings in fathoms at low-water mark.

PLATE VI.

Honolulu and its Fringing Reef. The line of breakers indicates the position of the outer slope of the reef. From a photograph.

PLATE VII

The eastern side of the entrance of Honolulu harbor. From a photograph. Diamond Head in the distance.

PLATE VIII.

The shore edge of the Fringing Reef, extending to the east of Honolulu harbor, towards Waikiki, with Diamond Head in the distance. From a photograph.

PLATE IX.

The rotten shore edge of the Fringing Reef east of Honolulu, near Waikiki. From a photograph.

PLATE X.

Passage cut through the shore edge of the Fringing Reef by the river coming down the Nuuanu Valley to the westward of Honolulu, seen from Smith Bridge. From a photograph.

PLATE XI.

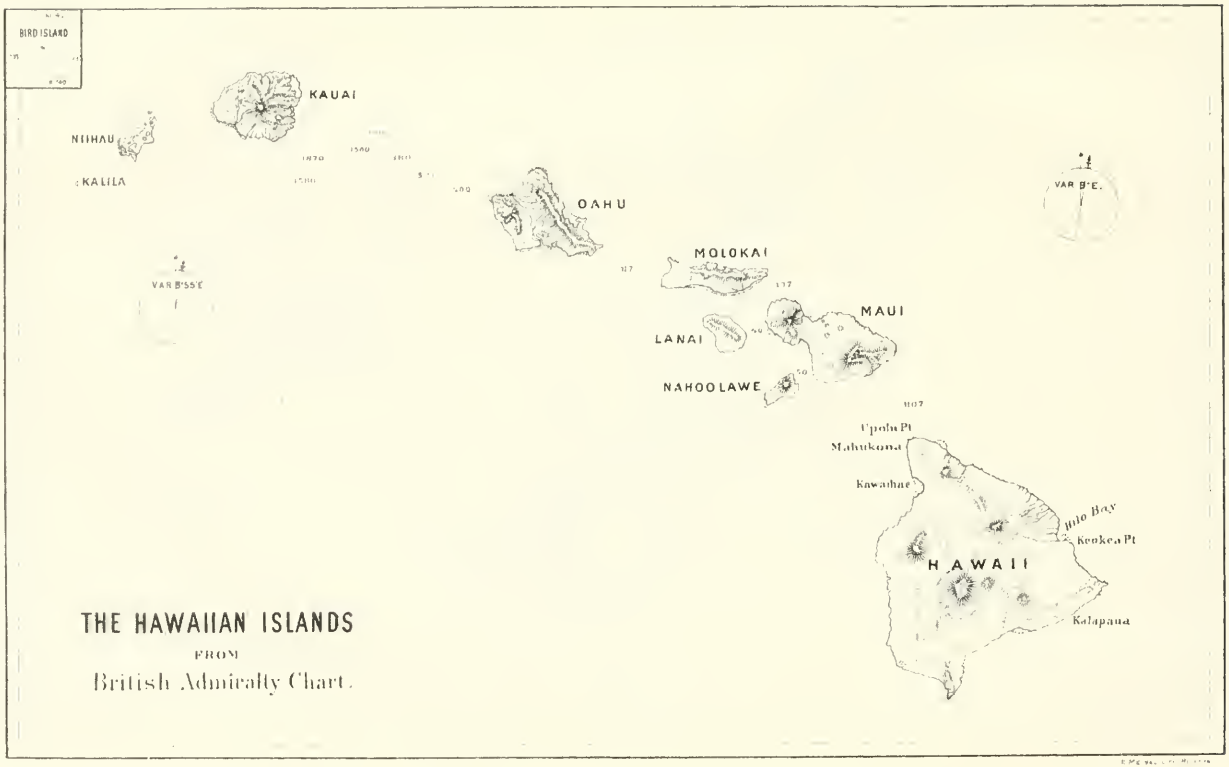
Pearl River Lagoon, the inshore arms of the Pearl Lochs. From a photograph.

PLATE XII.

Coral Sand Beach at Kahana formed from the triturated blocks of an ancient coral reef which once flourished between Kahana Bay and Kahuku Point. From a photograph.

PLATE XIII.

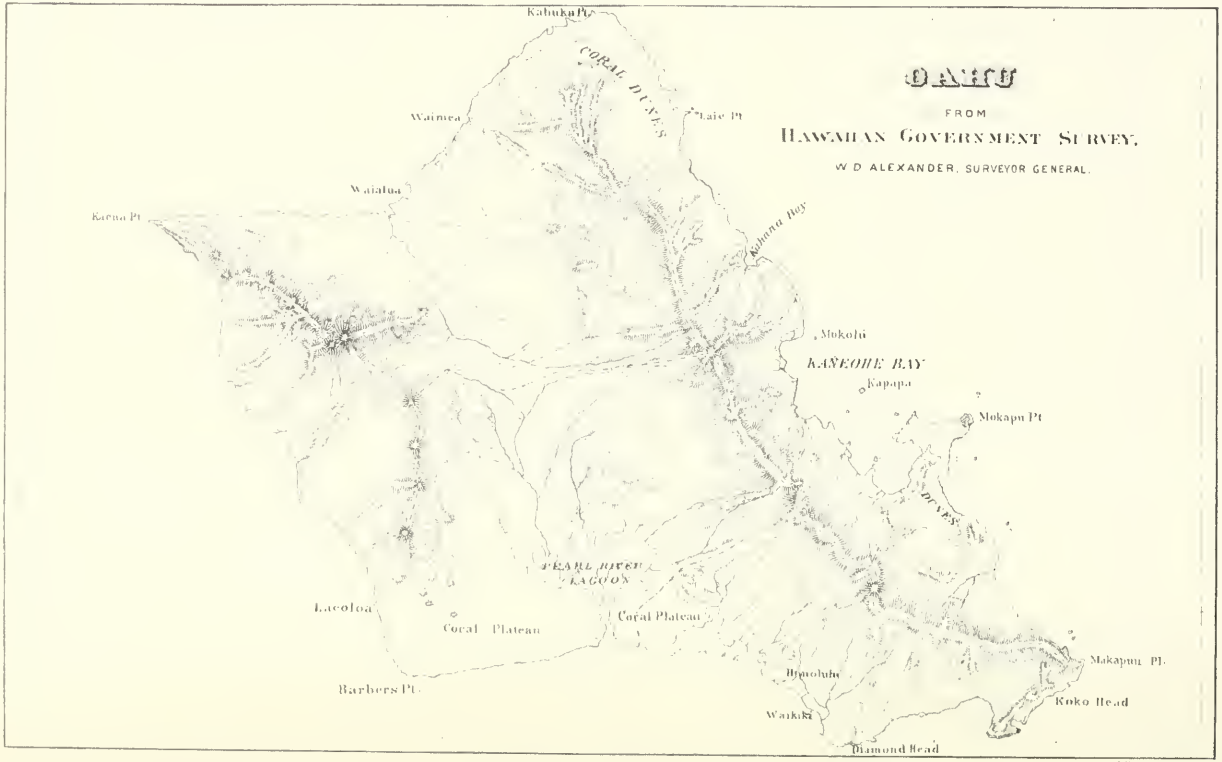
Sunken Coral Sand Beach at Kaimu, Hawaii. From a photograph.

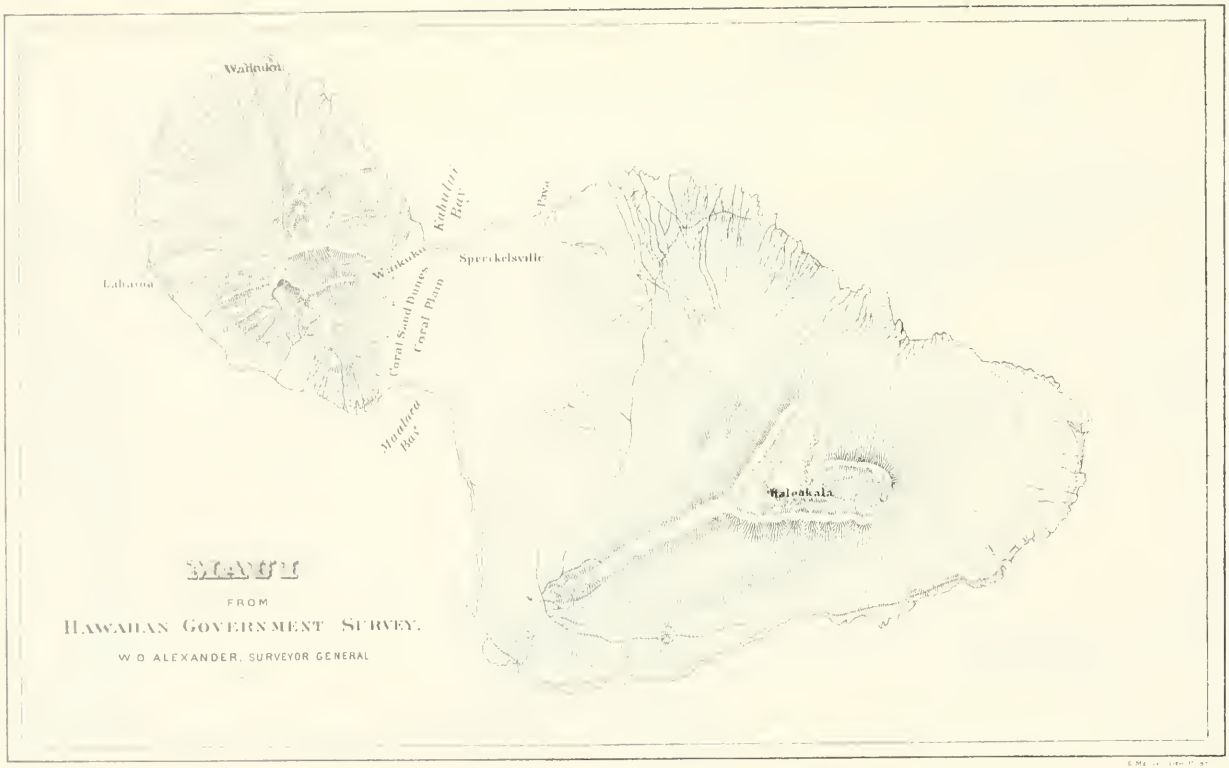


THE HAWAIIAN ISLANDS

FROM

British Admiralty Chart.


OAHU
FROM
HAWAIIAN GOVERNMENT SURVEY.
W D ALEXANDER, SURVEYOR GENERAL.
Kahuku Pt.
CORAL DUNES
Waimea
Laie Pt
Waialua
Kaena Pt
Kahuna Bay
Mokoli
KANEOHE BAY
Kapapa
Mokapu Pt
REEFS
PEARL RIVER LAGOON
Laeloa
Coral Plateau
Coral Plateau
Barbers Pt.
Honolulu
Makapuu Pt.
Koko Head
Waikiki
Diamond Head

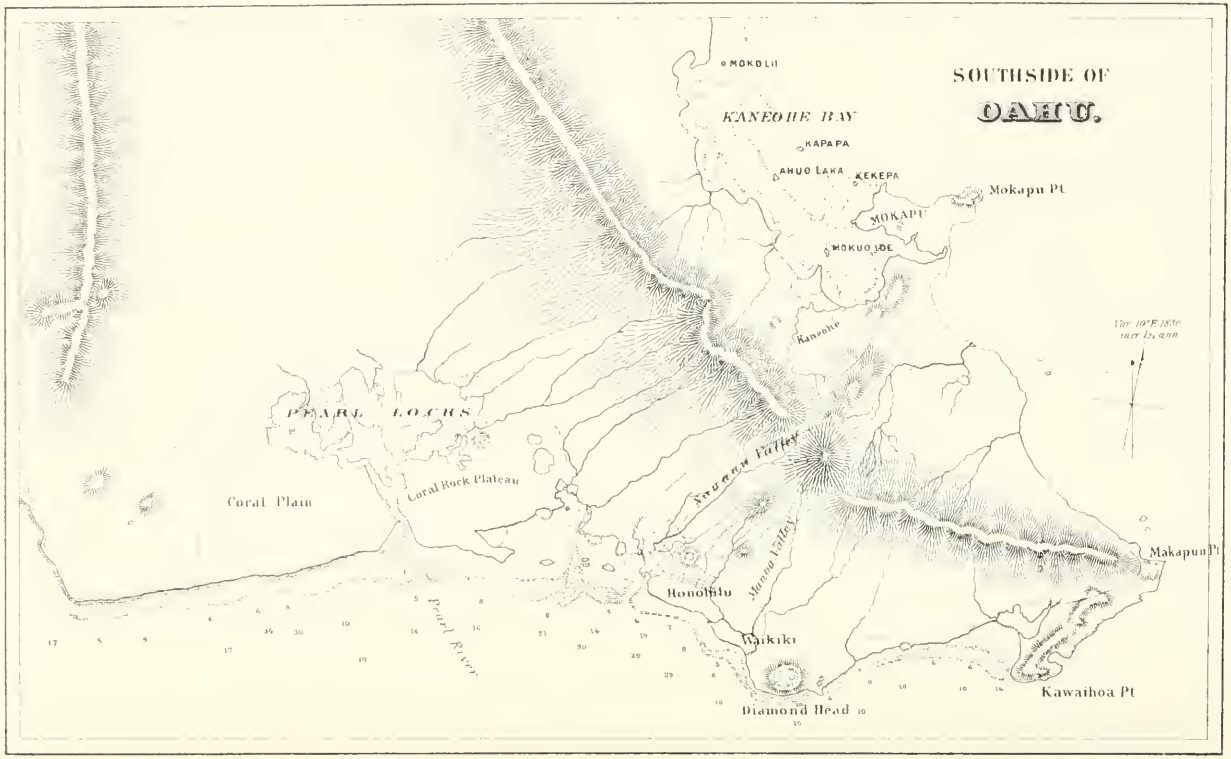


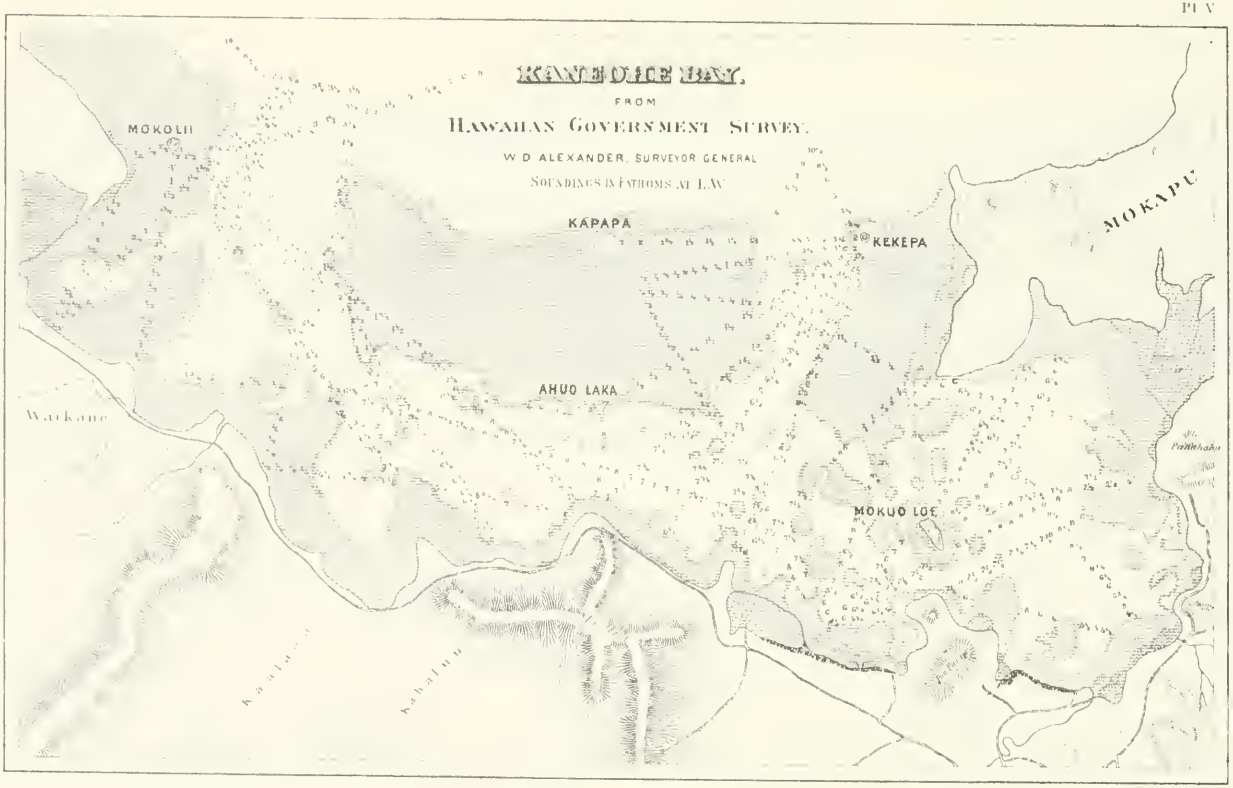
MAUI

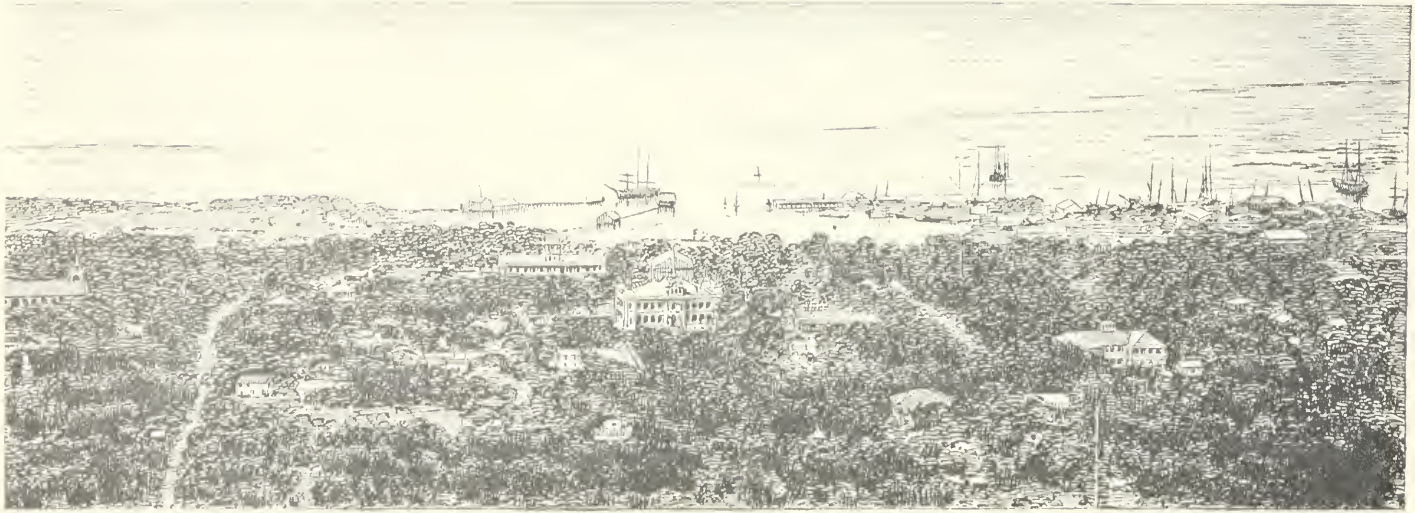
FROM

HAWAIIAN GOVERNMENT SURVEY.

W O ALEXANDER, SURVEYOR GENERAL


SOUTHSIDE OF
OAHU.
MOKOLII
KANEOHE BAY
KAPAPA
AHUO LAKA
KEKEPA
Mokapu Pt
MOKAPU
MOKUOLOE
Kaneohe
Var 10°E 1838
PEARL LOCHS
Coral Rock Plateau
Coral Plain
Nuuanu Valley
Manoa Valley
Makapuu Pt
Honolulu
Pearl River
Waikiki
Diamond Head
Kawaihoa Pt


KANEOHE BAY.
FROM
HAWAIIAN GOVERNMENT SURVEY.
W D ALEXANDER, SURVEYOR GENERAL
SOUNDINGS IN FATHOMS AT L.W.
MOKOLII
KAPAPA
KEKEPA
MOKAPU
AHUO LAKA
Waikane
MOKUO LOE
Kaalaea
Kahaluu

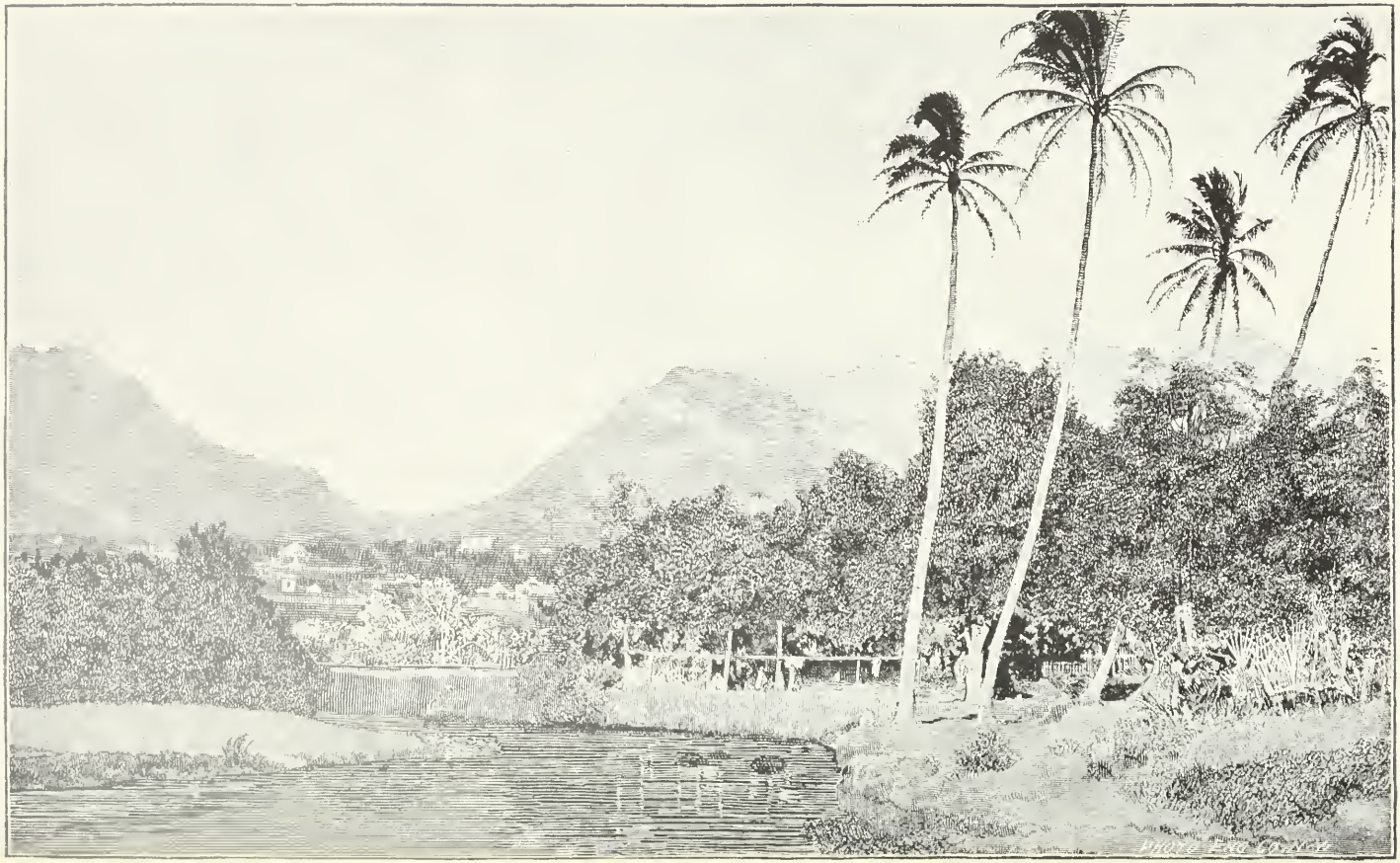


HONOLULU AND ITS FRINGING REEF.

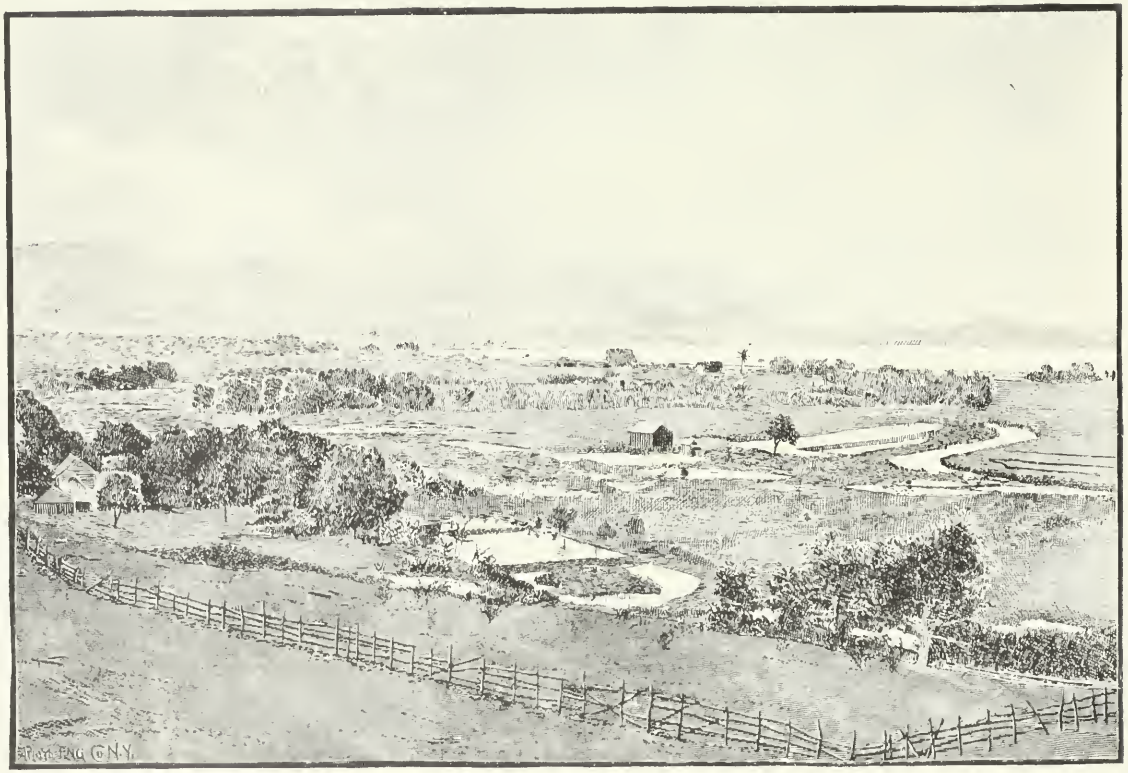
EASTERN SIDE OF THE ENTRANCE TO HONOLULU HARBOR.

SHORE EDGE OF THE FRINGING REEF EAST OF HONOLULU.

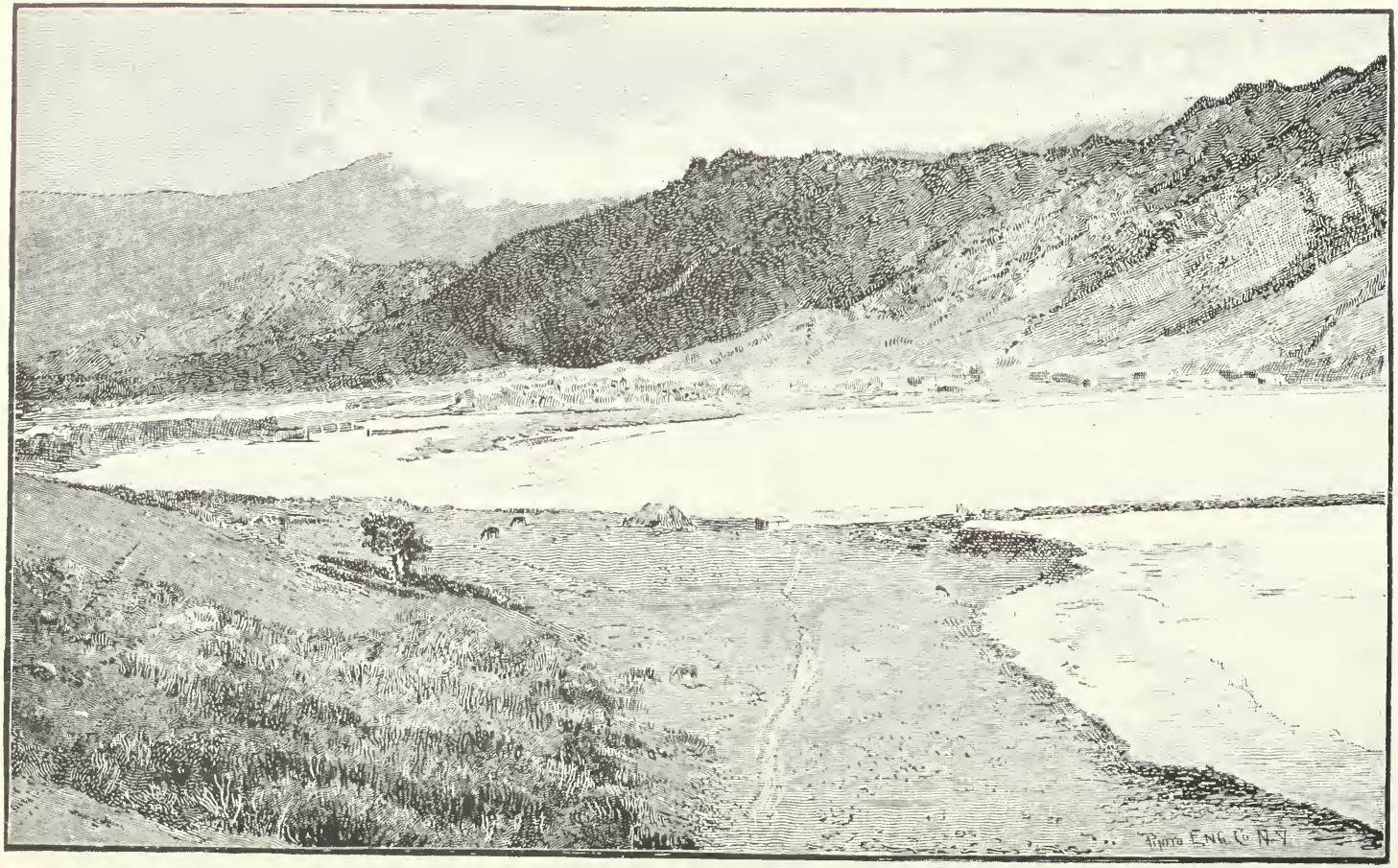
ROTTEN SHORE EDGE OF THE HONOLULU FRINGING REEF NEAR WAIKIKI.



PASSAGE CUT BY DRAINAGE OF NUUANU VALLEY THROUGH THE FRINGING REEF.



PEARL RIVER LAGOON.



CORAL SAND BEACH AT KAHANA.

SUNKEN CORAL SAND BEACH AT KAIMU.

No. 4. — *Studies on the Primitive Axial Segmentation of the Chick.*[1]

By Julia B. Platt.

A. — The Succession of the Protovertebræ.

While studying the general development of the chick in connection with my special work upon the segmentation of the medulla and the origin of the cranial nerves, I came upon the following sentence in Balfour's Comparative Embryology: "The first somite arises close to the foremost extremity of the primitive streak, but the next is stated to arise in front of this, so that the first formed somite corresponds to the second permanent vertebra."[2] A foot-note calls attention to the fact, that "further investigations in confirmation of this widely accepted statement are very desirable."

Prof. His is hardly more definite. He says: "Die Urwirbel, welche zuerst entstehen, sind, wie dies v. Baer bereits richtig erkannt hat, nicht die vordersten Halswirbel, sondern es bilden sich vor den zuerst entstandenen Wirbeln im 5 und 6 Stadium noch einige fernere. . . . Ich möchte mit v. Baer vermuthen, dass ihrer jederseits zwei entstehen, möglicher Weise ist indess diese Schätzung zu niedrig gegriffen."[3]

I believe that the "Photogramme zur Ontogenie der Vögel, von C. Kupffer und B. Benecke," is the only other publication in which there is either confirmation or refutation of the opinion advanced by Balfour, in regard to the order in which the protovertebræ are formed. From the explanatory remarks with which Kupffer and Benecke accompany their beautiful photographs of chick embryos, one is led to think that the first protovertebra to appear is at least the fifth in the series, counting from the anterior. In determining the order in which the protovertebræ arise, they have been principally guided by the difference in size found to obtain among the protovertebræ of the same individual. The largest is considered the first.

[1] These studies were pursued in the "Annex" Laboratory at the Museum of Comparative Zoölogy, Cambridge, Mass., under the direction of Dr. Howard Ayers. Zoöl. Laboratory, No. 14.

[2] Vol. II. p. 161.

[3] Untersuchungen über die Erste Anlage des Wirbelthierleibes, pp. 82, 83.

As my own investigations lead me to a conclusion at variance with that of Prof. Kupffer, I have examined the photographs with care, and am pleased to find that even in point of size the protovertebræ which I consider to appear first may well dispute the claims of Prof. Kupffer's first protovertebræ. In fact, the criterion of size among objects of such varying outline admits of a wide range of interpretation. It is not enough to judge from the superficial area, we must also take into account the depth. Moreover, it often happens that a large protovertebra appears opposite a small one, in which case size evidently does not determine seniority, since opposite protovertebræ are known to appear at about the same time. If precedence were established by size, then we should expect to find a gradual decrease in size from first to last; yet this is not what we do find, and Prof. Kupffer does not affirm that any protovertebra is second to be formed because second in size. Perhaps I am laying too much stress upon the matter of size, since what Prof. Kupffer says in this regard is quite conditional. He affirms only that, *if* size determines age, then we must consider this or that protovertebra first formed.

Moreover, it is not clear upon what Prof. Kupffer founds his opinion, that the second cleft in the mesoderm appears anterior to the first,[1] unless it be founded upon the relative distances of these two clefts from the anterior end of the primitive streak, as compared with the space which intervenes between the end of the primitive streak and the first mesodermic cleft in an embryo where only one cleft has yet appeared. This, at least, is the argument used in regard to Figure 25, *loc. cit.*, which represents a chick with four distinct pairs of protovertebræ, and a fifth faintly marked off in the mesoderm posterior to the others. Here the author considers the third from the anterior to be the one first developed, but allows that one might hesitate to decide between the third and fourth: "denn die Entfernung des hintersten Spalts von dem vorderen Ende des Primitivstreifs, harmonirt mit der Entfernung des ersten Spalts von demselben Punkte in den Figg. 20 und 22." (In Fig. 20 only one cleft has appeared in the mesoderm; in Fig. 22, there are but two.) "Mag man nun aber den einen oder anderen der beiden hinteren Urwirbel als den zuerst abgegliederten auffassen, jedenfalls geht aus den Figg. 24 und 25 hervor, dass die Segmentirung zunächst rascher nach vorn als nach hinten vorschreitet, und ist darnach die Angabe von Foster und Balfour zu berichtigen, die behaupteten dass die nächstfolgenden Urwirbel hinter dem ersten Paar entstünden."[2]

[1] Kupffer, p. 172.

[2] Ibid., pp. 173, 174.

Now, Figures 20, 22, 25, are said to be enlargements of the anterior portion of Figures 19, 21, 24, respectively. In the last mentioned figures, the distance from the posterior extremity of the primitive streak to the head fold varies but little, while the primitive streak alone, in that chick which has three or four more protovertebræ than the other two chicks, is shorter by the width of those protovertebræ. Comparing the pictures, and allowing for a difference in total length, we find that the *width* of three protovertebræ has been added in Figure 24 from the region of the primitive streak to that of the embryo, and this added space we find occupied by protovertebræ. This being the case, does it not seem quite reasonable to suppose that the posterior vertebræ are developed later than the anterior, in the space once occupied by the receding primitive streak, — especially since we know the important part played by the primitive streak in the formation of the mesoderm? I do not attach much value to this argument, nor do I know if it would hold true for other chicks which might be photographed; I would merely say that these three photographs, which are compared by Prof. Kupffer for the purpose of determining the first protovertebra, are capable of leading to conclusions quite different from those at which the author arrives.

Prof. Kupffer further remarks: "An den Figg. 33 und 34 sind einige Einzelheiten hervorzuheben. Man geht wohl nicht fehl, wenn Man das in der Contourzeichnung mit *u'* markirte Urwirbel-paar [of five pairs, the fourth] als das erst entstandene auffasst. Abgesehen von der Grösse [it does not seem to me larger than either the second or fifth pair] spricht der Umstand dafür, dass die Axe der Urwirbel dieses Paares nicht senkrecht auf der Medianlinie steht, sondern eine leichte Neigung noch hinten zeigt. Es harmonirt das mit der Richtung der beiden ersten Spalten, Figg. 19–22."[1] Let me call attention to the fact, that the fifth pair of protovertebræ in Figures 33 and 34 shows also a "Neigung nach hinten," but is evidently not therefore considered "das erst entstandene."

I allow, indeed, that the obliquity of the angle made by the fourth and fifth pairs of protovertebræ with the main axis of the chick in Figures 33 and 34 corresponds well with the obliquity of the angle in Figures 19 and 22, where, as will be remembered, but one pair of protovertebræ is developed, and there is therefore no doubt about its being the first; but how in regard to Figure 23, where "der erste Urwirbel ist . . . deutlich begrenzt, vor demselben ein zweiter und hinter dem

[1] Kupffer, pp. 175, 176.

ersten ein dritter in der Abgrenzung begriffen"?[1] Here the second pair of protovertebræ, the only pair as yet distinctly formed, is quite at right angles with the main axis of the chick, while the only one obliquely placed — the posterior — is not as yet fully formed, and therefore cannot be the first formed. Thus we see that, where there is but one pair of protovertebræ, it makes an oblique angle with the middle line; where there are three pairs, the third as yet but half defined protovertebra is oblique; and where there are five pairs, obliquity belongs to the last two pairs, of which the fifth is not as yet distinctly separated from the surrounding mesoderm. It seems, therefore, reasonable to suppose that the characteristic of obliquity to the middle line belongs rather to the protovertebra just formed, or forming, than to the protovertebra which of any given number was first formed.

Figure 41 represents a chick with seven pairs of protovertebræ, of which the fifth is marked as first. Figure 50 represents a chick with nine pairs, of which the fourth is designated first; and the author naively remarks, that "das Bild (Fig. 50) ist aufgenommen worden, um an einem zweiten Beispiele die Constanz der Erscheinungen an den Urwirbeln zu demonstriren." Four pairs of protovertebræ developed in front of the first in the less advanced chick; three pairs developed in front of the first in the more advanced chick. Shall we not call this variation, rather than constancy? I think enough has been said to show that neither the size of the protovertebræ, their relative distance from the primitive streak, nor yet their obliquity to the main axis, is a sufficient ground to warrant a decisive answer to the question in regard to the order of their development.

It may be that Prof. Kupffer has other reasons than those which he mentions for thinking it highly probable that the fourth or fifth pair of protovertebræ is the pair first developed; but in so far as the arguments he advances are concerned, one may well hesitate to accept his conclusions until they be supported by further evidence.

I have studied one hundred and fifty or more chicks, and from their external appearance I have been able to make out little in regard to the order in which the first protovertebræ are formed. The length of the chick at this early stage varies; the shape and relative length of the primitive streak vary; the outline of the area pellucida is seldom exactly the same in any two chicks. In fact, there seems to be no fixed point from which to measure. But I have been more fortunate in the study of serial sections. From these I learn that the cleft which sepa-

[1] Kupffer, p. 172.

rates two protovertebræ is not at the time of its first appearance a continuous break extending throughout the width and depth of the vertebral plate. As a first trace of segmentation, there appears, in a line transverse to the axis of the chick, a succession of slight depressions on the dorsal surface of the vertebral plate. In a series of sagittal sections these depressions appear and disappear, a single depression seldom occupying more than two or three sections. As the chick grows, these depressions gradually deepen and become more continuous, while immediately below them a slight upward curve appears in the ventral boundary of the mesoderm. A little later, a distinct line appears, connecting these two indentations, and separating the cells of the undifferentiated mesoderm from those which are about to form a protovertebra. The latter now take on the spindle shape that characterizes the protovertebral cell, their long axes becoming gradually radial as regards the protovertebral body. Soon there appears here and there a break in the line that bounds the forming protovertebra, but, as a rule, cell prolongations, in a horizontal plane somewhat below the middle of the protovertebra, bind the new protovertebra, on the one hand to the undifferentiated mesoderm, and on the other to the protovertebra last formed.

The formation of a distinct and separate protovertebra takes place so gradually that a single long section shows the process in all stages of progression. Passing from the fully formed protovertebræ through four or five in process of formation, one reaches the undifferentiated mesoderm, in which a faint dorsal depression gives the first indication of the place where a protovertebra will ultimately be cut off.

This being the case, it is evident that, provided the order in which the protovertebræ are formed is in every chick the same, and provided that a protovertebra which has once started to develop continues to develop regularly, then, to determine the order in which they have developed requires but a sufficiently complete set of sectioned embryos.

In development, as in adult life, individual chicks may be expected, within a certain limited range, to vary from the typical chick. Still, if we find certain conditions to prevail in a large number of chicks, without exception, we are warranted in assuming these conditions to be normal. The protovertebræ are not formed until the mesoderm in the region of the somites has grown to be quite compact, and is as many as four cells deep, so that when the cell layers first take on their concentric arrangement they lie in two layers about the central axis of the protovertebra. I have never seen a protovertebra whose walls were

but one cell thick, hence I am warranted in assuming that a certain thickness pertains to the mesoderm from which a protovertebra is immediately to be formed. Since the breaks in the mesoderm appear so gradually, it is possible, at the time the first cleft has appeared, to see where the next is to follow, and consequently to determine definitely on which side of the first protovertebra the first cleft appeared.

Figure 1, Plate I., is a section through a chick at the time when one decided parting of the mesoderm occurs, and the chick when examined entire by transmitted light showed but one mesodermic cleft.

From this section it will be seen that the first cleft lies anterior to the first protovertebra, not posterior, as Kupffer and Benecke supposed. A partial cut separates this protovertebra from the posterior mesoderm, while the protovertebra anterior to the first cleft is still closely connected with the mesodermic band which runs forward to the head. In fact, the anterior protovertebra is not entirely separated from the anterior mesoderm until as many as four or five protovertebræ have been formed. A curve in the dorsal outline of the mesoderm indicates from the first, however, where the anterior protovertebra is to be ultimately cut off. The series from which Figure 1 is taken shows more conclusively than any other series which I have, the relation of the first mesodermic cleft to the first protovertebra. It is difficult to find the exact stage when the first cleft is far more developed than the second, although the second one is already distinctly marked. However, in almost any series made at the time when the first protovertebra has just been formed, the same conclusion with regard to the priority of the anterior cleft may be reached by comparing the number of entire and partial breaks which occur in successive sections anterior to the first protovertebra with those that occur posterior to it. It will then be found that the anterior cleft is both deeper and more continuous than the posterior. The sections which I have drawn have been selected from chicks, the stages of whose development follow so closely upon one another, that, if it be supposed that between any two stages the protovertebra marked *a* has developed into that marked 1, while the cells included between the letters *f* and *g* have developed into the protovertebra *a*, then the protovertebræ, which in the preceding section were already partly cut off, posterior to 1, must have become attached to the mesoderm from which they were thus partly separated, or the order of development must vary in different chicks ; for if the above supposition were true, in the chick with the greater number of protovertebræ the posterior ones would be less

distinctly set off than in the chick with a less number of protovertebræ. The sections, however, do not support this supposition, since they show that, while the undifferentiated mesoderm posterior to the first protovertebra (1) is of the requisite thickness to permit of the formation of protovertebræ, the mesoderm anterior to *a* is too thin. This I find to be the case in all chicks which I have examined at this stage of development. Aside from the thinness of the mesoderm anterior to protovertebra *a*, the sections also show that even in the anterior part of *a* the cells have not increased as rapidly as in the posterior part. Consequently, this protovertebra is characterized by a peculiarly asymmetrical form, which gives it, in the early stages of its growth, an appearance quite different from that of the other protovertebræ. (See Figs. 2, 3, 4, and 6.)

Figures 5 and 5 a are taken from a series which was not cut parallel to the axis of the chick, and therefore the appearance of protovertebra *a* in Figure 5 is delusive. These facts force me to conclude that, contrary to the opinion advanced by Kupffer and Benecke, the development of protovertebræ is much more rapid caudad than cephalad. Indeed, after the first cleft in the mesoderm appears, dividing two forming protovertebræ, the posterior mesoderm goes on continually differentiating into protovertebræ until the chick acquires its complete number of protovertebræ, while it is only after three or four protovertebræ have been thus formed posterior to the first, that protovertebra *a* becomes finally separated from the anterior mesoderm, after which this mesoderm also slowly acquires sufficient thickness to form another protovertebra anterior to *a*.

Figure 5 a was drawn for the purpose of showing a group of cells lying between *f* and *g*. They come into section near the outer (i. e. lateral) boundary of the line of protovertebræ, and extend through only three sections, while it takes twenty sections to pass through a protovertebra. They are, in fact, the first indication of the formation of a protovertebra anterior to *a*. A like group of cells is not found on the opposite side, nor do they occur on either side of the chick from which Figure 6 is taken. But I find a similar group of cells in the same position (between *f* and *g*) in the series from which Figure 7 is drawn. The section represented is that which shows best the characteristic radial arrangement of these cells. Here, too, but few sections pass through the group. In the succeeding stages they are more marked, and by the time five or six protovertebræ have been formed posterior to 1 these cells have become distinctly *protovertebral* in their arrangement.

Still the new protovertebra is little more than a half-protovertebra, for it is much smaller than those immediately behind, and opens anteriorly to the mesoderm of the head, into which it passes with no distinct boundary. These peculiarities of protovertebra *b* are evident even in the entire chick, if examined at this stage.

For some time I thought it possible that this incomplete protovertebra might be formed from protovertebra *a*, but this cannot be the case, for I have traced its growth from a few cells grouped together anterior to *a*, up to the time when the ninth nerve, passing behind the ear capsule, crosses so near to this protovertebra as to leave no intervening tissue from which another protovertebra could be formed. That another protovertebra is not formed anterior to *b* is also evinced by the fact, that in no subsequent stage does the line of protovertebræ end anteriorly in a *complete* protovertebra, or in a protovertebra *less complete* than *b*. If *b* became complete, and the tissue anterior to *b* developed into an incomplete protovertebra, it would be possible to find the stage in which this change took place.

In Kölliker's "Entwicklungsgeschichte des Menschen und der höheren Thiere," there is a figure [1] representing an "Urwirbel ähnlicher Körper *vor* der Gehörgrube, der von einem Ganglion und zwei Nerven gebildet wird." Another figure [2] represents an embryo with two large cell masses at the beginning of the protovertebral line, which Kölliker calls "Urwirbeln ähnliche Massen." He supposes them to represent the "vereinigte Anlage der Ganglion des Glossopharyngeus und Vagus." The shape of these last mentioned protovertebra-like structures, and their relative distance from the ear capsule, lead me to think it highly probable that their posterior wall is formed by the incomplete protovertebra (*b*) of which I speak above, while their anterior wall is formed by the ninth nerve. However this may be, since Kölliker affirms these structures to be at least in part *ectodermic*, they offer no objection to the limitation which I place upon the *mesodermic* protovertebræ, of which alone I speak.

My conclusions are, therefore, that the first break in the mesoderm occurs anterior to the first protovertebra, and that two protovertebræ (or, more correctly, one and a half) are slowly formed anterior to the first mesodermic cleft, in the time occupied by the formation of six or seven protovertebræ posterior to that cleft. With regard to the number of protovertebræ occurring anterior to the first, my work confirms the estimate of His and Von Baer.

[1] *Loc. cit.*, p. 430.

[2] *Loc. cit.*, pp. 142, 143.

In respect to the further development of these protovertebræ, I quote from Froriep,[1] the results of whose investigations have been corroborated by Van Wijhe. "In der Occipital region, *d. h.* in dem zwischen ersten Cervical-nerven und Vagus eingeschlossenen Abschnitt der Wirbelsäule, finden sich bei viertägigen Hühnerembryonen vier Muskelplalten, welche von hinten nach vorn (cranialwärts) an Grösse abnehmen. Es waren also hier vier Urwerbel angelegt, welche in den Aufbau des Kopfes eingehen. Der fünfte liegt auf der Grenze von Kopf und Halswirbelsäule, die Muskelplatte, die dieser liefert, berührt mit ihrem caudalen Rand die Anlage des ersten Halswirbelbogens, mit dem cranialen die hinterste Bogenanlage der Occipitalgegend."

We see, therefore, that the first mesodermic cleft divides evenly the four pairs of protovertebræ which enter into the formation of the head, and that this cleft does not coincide with the occipito-cervical cleft of the adult.

B. — The Relation of the Cranial and the Spinal Nerves to the Neural Axis.

The development of the rudimentary protovertebra *b* brings me to that stage in the growth of the chick with which my work ostensibly began. Contemporaneously with the formation of this protovertebra, the successive constrictions of the medulla appear, the neural crest is formed, and the first cranial nerves arise (V., VII., VIII.).

If a chick be examined by transmitted light during the second or third days of incubation, it will be noticed that the medulla is marked by a series of swellings and constrictions which are directly continuous with a line of similar swellings and constrictions in the region of the spinal cord. These divisions of the medulla are such noticeable characteristics that they have frequently been mentioned before the comparatively recent attempts to determine the number of head-segments from the distribution of the cranial nerves. His, Rabl, and Balfour speak of them as more or less transitory structures; but in so far as I know, Béraneck and Orr are the only authors who have attempted to elucidate by their means the problem of cranial segmentation.

In an article upon the cranial nerves of the Lizard,[2] Béraneck describes five successive enlargements of the central canal of the

[1] Archiv Anatomie und Physiologie, 1883. Zur Entwickelungsgeschichte der Wirbelsäule, p. 226.

[2] Des Nerfs Crâniens chez les Lézards. Recueil zoologique Suisse, 1884.

medulla, corresponding to which the external surface of the neural wall is marked by five encircling swellings. These he designates "replis médullaires," (designated by Dr. Orr "neuromeres,") and he attempts to assign to them a segmental value, from their constant relation to certain of the cranial nerves. With the anterior neuromere he finds the fifth nerve connected; with the third, the united seventh and eighth nerves, while the roots of the ninth nerve come from the fifth neuromere.

Dr. Orr, in a recent publication upon the development of the Lizard,[1] gives a similar description of the relation existing between the neuromeres (replis médullaires) and the fifth, seventh, and ninth cranial nerves. Béraneck has also published a detailed account of the neuromeres in the chick,[2] and has assigned to each fold a segmental value. The two anterior folds correspond to the two head-segments supplied by the fifth nerve. The third neuromere belongs to the united seventh and eighth nerves, these nerves consequently representing but one primitive segmental nerve. The fourth neuromere he assigns to the segment of the auditory capsule and sixth nerve, believing the relation which obtains between the auditory capsule and eighth nerve quite secondary. The fifth neuromere is connected with the ninth nerve. The tenth nerve represents a transitory condition between a spinal and cranial nerve, and is consequently not entitled to its neuromere, since the swellings and constrictions in the region of the spinal cord are not considered by Béraneck structures homologous with the neuromeres.

Béraneck claims to have found similar folds in tritons and elasmobranchs, although he was deterred from establishing their relation to the cranial nerves by lack of material. To the above list of vertebrates possessing neuromeres, I can add the salmon. Between the ages of fourteen and nineteen days the medulla of the salmon is divided into five distinct lobes or neuromeres, with the anterior of which the fifth nerve is connected; with the third, the ganglion of the seventh and eighth nerves, while the ninth nerve passes from behind the ear capsule close to the fifth neuromere. I did not have sufficient material, at the age when the nerves first appear, to decide whether this relation between nerves and neuromeres is primitive or secondary. From the constancy with which *five* neuromeres appear in classes so widely separated as fish, reptile, and bird, they would seem to be structures inherited from a common ancestral form. Moreover, the constancy in the number of

[1] Embryology of the Lizard. Journal of Morphology, 1887.

[2] Replis Médullaires du Poulet. Recueil zoologique Suisse, 1887

neuromeres is not less striking than the constant relation which the first, third, and fifth neuromeres bear to the fifth, seventh, and ninth cranial nerves.

The constrictions which in the chick divide the neural tract into cerebral vesicles or "neuromeres," appear even before the neural walls have formed a closed canal. They arise successively from before backwards, dividing the medullary tube into vesicles, which decrease in size in the order of their formation. The third neuromere of the medulla (fifth vesicle formed) is the only exception to the gradual diminution of the successive vesicles. This neuromere (Fig. 17, Plate II.) is smaller than either the second or fourth.

Anterior to the first protovertebra the neural canal is divided by a series of such constrictions into seven vesicles. With the appearance of each successive protovertebra, another constriction occurs opposite the protovertebra, and another neuromere (as we may also designate these neural swellings) is added to the preceding. The constrictions of the spinal cord often appear before the formation of the corresponding protovertebræ; consequently these ectodermic differentiations are quite independent of any mechanical influences consequent upon the formation of the protovertebræ.

Béraneck has already carefully described and figured the medullary folds, and in as far as the folds themselves are concerned I can but confirm the results of his investigations; yet I have ventured to repeat the description in brief, because I would call attention to the fact, that in the chick, at least, the order in which the various parts of the brain are formed does not correspond with what is usually given as the typical development of the vertebrate brain.

Wiedersheim says: "At a very early stage three swellings may be seen on the anterior enlarged part of the medullary tube, which are spoken of as the primary anterior, middle, and posterior cerebral vesicles (fore-, mid-, and hind-brain). . . . The primary fore-brain and hind-brain each become differentiated into two parts, and thus five divisions of the brain may be distinguished. Counted from before backwards, these are Prosencephalon (secondary fore-brain), Thalamencephalon (primary fore-brain), Mesencephalon (mid-brain), Metencephalon (secondary hind-brain), and Myelencephalon (primary hind-brain)."[1] I quote from Wiedersheim, because he expresses so concisely the opinion commonly advanced by zoölogists in regard to the formation of the vertebrate brain.

[1] Comparative Anatomy of Vertebrates, pp. 131, 132.

From Figure 17, Plate II., it will be seen that the primitive brain of the chick does not correspond with the above description. As the result of my studies, I find that primarily the chick's brain consists of a succession of neural vesicles, from the first of which the three anterior divisions of the adult brain are developed, namely, Prosencephalon, Thalamencephalon, and Mesencephalon. Soon after the formation of the first cerebral vesicle, the optic lobes appear as lateral outgrowths from it, after which, for some time, the growth of this vesicle is not relatively greater than the growth of the following vesicles, or than that of the entire embryo. But with the first appearance of the cranial flexure, the primary fore-brain begins to develop very rapidly, soon a constriction marks off the mid-brain (Fig. 15), after which the fore-brain grows out as an anterior vesicle, so that by the time the head is completely bent, the primary fore-brain is represented by three large vesicles, which open widely into each other (Fig. 14). The development of these three vesicles is wonderfully rapid, and since it is exactly coincident with the cranial flexure one may well connect the two events causally, affirming the cranial flexure to result from the very rapid development (increase of surface) of the dorsal and lateral walls of the first cerebral vesicle.

The second primary vesicle develops into the cerebellum, and the successive vesicles, including the neural swellings between the first five protovertebræ, take part in the formation of the adult medulla oblongata. Thus, either the development of the brain in the chick forms a marked exception to the usual development of the vertebrate brain, or the nomenclature of the three primary cerebral vesicles is inaccurate. The prevalent impression, that the brain consists primarily of but three vesicles, may possibly arise from the fact that the ectoderm does not exactly follow the neural conformation. The surface of the head at an early stage presents three main divisions, marked by slight constrictions, but these are quite independent of the neural tract. The difference between the contour of the head and that of the brain will be manifest if the chick be first examined as an opaque object, and then by transmitted light. In the former case, the superficial outlines of the head are most apparent; in the latter, the medullary walls come into strong relief.

Although I agree with Orr and Béraneck in regard to the number and appearance of the neuromeres, and although I also find the ultimate relation of the cranial nerves to these folds in salmon and chick to be the same as that which they describe for lizard and chick, I do *not*

find that this relation is a primitive one in the chick. From lack of material, I was unable to study the younger stages of development in the salmon; but with regard to the chick, I can say definitely that at its first appearance the fifth nerve does *not* arise from the outward convexity of the first neuromere of the medulla, as Béraneck has represented it. It arises from the concavity that lies between the first and second neuromeres, and its position at the side of the anterior neuromere is quite secondary. This fact supports Marshall's theory, that segmental nerves "at an early period shift downwards, and acquire new or secondary roots of attachment to the side of the brain."[1] It has seemed to me that the secondary attachment of the fifth nerve was not due to a new outgrowth connecting the nerve root and brain, but rather to a gradual shifting of the position of the original root. However this may be, it certainly cannot be owing to the outward spreading of the walls of the fourth ventricle that the root of the fifth nerve comes to acquire an attachment anterior to its primitive attachment. Béraneck says: "Par suite des changements survenus dans la roûte du cerveau postérieur, . . . les replis sont encore plus déjetés sur les côtés de la région céphalique et les racines nerveuses paraissent être descendues et se rattacher plus près de la région ventrale qu'auparavant. . . . Les changements survenus dans la forme et la structure du cerveau postérieur me semblent suffire à expliquer cette descente apparente des nerfs crâniens sans qu'il faille recourir à une hypothèse ne reposant sur aucune observation directe."[2] The mere divergence of the walls of the fourth ventricle may suffice to explain the more ventral attachment of the fifth nerve, but is hardly sufficient to account for the fact that its secondary attachment is anterior to the first.

Since the walls of the fourth ventricle follow quite closely the curves on the outward surface of the medulla, the concavity from which the fifth nerve arises is represented on the inside by a ridge projecting far into the fourth ventricle. A series of horizontal sections through the root of the fifth nerve at the time of its attachment between the first and second neuromeres shows this ridge to be composed of lines of cells converging like the rays of a fan towards the point from which the fifth nerve takes its origin (Fig. 10). This convergent arrangement of lines of cells is characteristic of each of the ridges which, projecting into the fourth ventricle, separate successive neuromeres (Fig. 12 b). If

[1] A. Milnes Marshall. Segmental Value of the Cranial Nerves. Journal of Anatomy and Physiology, 1882.

[2] Replis Médullaires du Poulet, Rec. zool. Suisse, pp. 334, 335.

Figure 10 be examined, it will be seen that the fifth nerve draws its fibres from both the posterior part of the first neuromere and the anterior part of the second. Succeeding sections show the connection between the nerve and the neuromeres, both anteriorly and posteriorly, to be more extensive than in the section drawn. Béraneck says, apropos of the connection between the fifth nerve and second neuromere: "J'avais toujours été frappé de ce que la seconde paire des replis médullaires était la seule ne paraissant avoir aucune relation avec les nerfs crâniens. En étudiant la question d'un peu plus près je reconnus que cette deuxième paire émet un tronc nerveux qui vient se fondre avec celui partant de la première. Ainsi les éléments qui constituent le trijumeau sont fournis par les deux premières paires des replis médullaires. . . . Le trijumeau correspondant à deux paires de replis, ne serait donc pas un nerf simple, mais résulterait de la fusion de deux troncs nervaux primitivement indépendants." [1]

From the fact that the second neuromere, as well as the first, contributes fibres to the formation of the fifth nerve, I cannot argue, as Béraneck does, that these two neuromeres correspond to the two primitive segments to which, from its peripheral distribution, the fifth nerve is supposed to be related.

Of the two segmental nerves united in the fifth, one is surely represented by the main branch of the fifth with its Gasserian ganglion, the other segmental nerve is usually supposed to be represented, at least in part, by the ramus ophthalmicus profundus, with its ciliary ganglion. In fact, Van Wijhe claims to have traced in the elasmobranch the backward growth of the ramus ophthalmicus, from its connection with the brain in the immediate neighborhood of the ciliary ganglion to its final fusion with the main body of the fifth nerve. This being the case, one would hardly look for the neuromere of that anterior segmental nerve, which has thus lost its independence, back of the neuromere to which the fifth nerve is itself attached. It is possible, indeed, to suppose that the whole fifth nerve has transferred its connection from the posterior to the anterior neuromere, but such a supposition takes away any segmental value which may attach to the neuromeres from their present relation to the cranial nerves.

Aside from any theory of segmentation, the fact remains that the fifth nerve, at the time of its origin, arises from the depression between the first and second neuromeres, while the cells composing its root are intimately connected with the cells forming the mass of the ridge which

[1] *Loc. cit.*, p. 337.

projects into the fourth ventricle, opposite the external attachment of the nerve. It is therefore with this inner swelling, and not with an outer one, that the fifth nerve is originally connected. It may here be noticed, that neither the third nor fourth cranial nerve arises from the middle of the vesicle with which it is connected, but both are attached to the brain near the line which separates this vesicle from the following.

Passing from the concavity between the first and second neuromeres to that which separates the second and third, or, in other words, passing from the first medullary ridge (using this term to designate the internal ridges) to the second, we come to the origin of the seventh nerve, anterior to the small neuromere beside which lies the ganglion of the united seventh and eighth nerves. In a series of horizontal sections made at the time when these nerves have just left the neural crest, it will be found that from each side of the third neuromere nerve fibres pass downward and towards the middle of that neuromere, where they unite in a large ganglion. (See Fig. 12 b.) This ganglion is ultimately and secondarily connected with the convexity of the third neuromere. As I remarked above, this neuromere is smaller than any other anterior to the origin of the tenth nerve, consequently the space included between the large roots of the seventh and eighth nerves is small, and might easily be overlooked in transverse or sagittal sections. (See Fig. 12 a.) The long axes of the cells composing each nerve are, as usual, parallel to each other, but since the two nerves meet the ganglion from different directions, it follows that the long axes of the cells composing the seventh nerve make an angle with the long axes of those composing the eighth nerve, and the ganglion is consequently connected with the brain by two bands of cells whose long axes diverge (Fig. 12 a.)

Although the fibres of the ninth nerve lie in close proximity to the fifth neuromere, they may be traced back of the ear capsule to the concavity which separates the fourth and fifth neuromeres, and corresponds to the fourth medullary ridge. (See Figs. 11 and 11 a.) The first figure shows the course of the nerve, and passes through the neural crest. The second figure is drawn to show the relation of the nerve to the entire ear capsule and the medullary ridge. They are from the same series.

Posterior to the ninth nerve, the long commissure of the tenth nerve extends beyond the fourth protovertebra. The peripheral distribution of this nerve, and the extent of its commissure, show it to be composed of the fused roots of several spinal nerves. All of the spinal nerves arise opposite the muscle plates (Figs. 13, 13 a) from correspond-

ing concavities in the spinal cord. The nerve fibres primarily connecting the spinal ganglia with the cord, form an almost continuous sheet extending along each side of the spinal cord. At intervals corresponding to the interspaces between the protovertebræ, these fibres are apparently pushed to either side by the thickened mesoderm which projects upward from the region of the notochord, so that the fibres between every two such mesodermic thickenings are drawn into one spinal ganglion. The width, therefore, of the band of fibres connecting a spinal ganglion with the spinal cord, corresponds to the width of the protovertebra lateral to it (Figs. 13, 13 a). From a glance at the general relation of the neural concavities to the nerves which arise from them, it will be noticed that, where the ganglion is connected with the neural axis by a mass of fibres bound closely together, the curve of the concavity from which they arise is sharp, as in the region of the medulla. Where the fibres are spread out, forming a wide ganglionic connection, the curve of the concavity is gentle, as in the spinal cord. But whether its curve be gentle or sharp, the concavity in both medulla and spinal cord is the source from which the nerves originate, and the neural swellings which correspond to the nerve roots are the inner ridges, not the outer neuromeres.

Béraneck is unwilling to homologize the neuromeres of the medulla with the swellings of the spinal cord, because of the difference in the later differentiation of the nervous tissue in these two regions, and because, as he affirms, the swellings of the spinal cord are transient. But so are also the neuromeres of the medulla. By the fifth day of incubation they are fast fading away, yet at this time the wave-like form of the walls of the spinal cord is still plainly visible (Fig. 13). Here, as in the medulla, the segmentation is more manifest in the ventral region than in the dorsal. Moreover, at the time when the neuromeres of the medulla and the swellings of the spinal cord first appear, the tissue throughout the neural tract is quite indifferent. Further, since the first four folds posterior to Béraneck's *five* medullary folds lie also in the region of the medulla, and are also connected with a cranial nerve, — viz. the tenth, — it is practically impossible to draw the line separating these folds from the more anterior. It is true that they are smaller, but the difference between the fifth neuromere and the next posterior fold is not as great as the difference between the second and third neuromeres. I therefore see no reason why the successive swellings which originally mark the neural tract should not be regarded as homologous structures.

Orr says: "Balfour described certain internal swellings of the lateral wall of the hind-brain of elasmobranch embryos: 'Swellings of the brain towards the interior of the fourth ventricle are in connection with the first five roots of the vagus and the glosso-pharyngeal root, and a swelling is also intercalated between the first root of vagus and the glosso-pharyngeal root.' In his figure (Fig. 5, Pl. XVI., *l. c.*) there are no external marks of these divisions, and the 'swellings' lie opposite the nerve roots while in the region between the nerve roots there are internal depressions. In the lizard, on the contrary, in the region between the nerve roots are internal ridges. The two conditions are thus very different; but possibly younger elasmobranch embryos might show a connection between these swellings and neuromeres."[1] My experience with the chick leads me to believe that possibly younger stages in the development of the lizard than those which either Orr or Béraneck was able to study may show a connection between the "swellings" and the nerve roots.

[1] *Loc. cit.*, pp. 336, 337.

July, 1889.

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EXPLANATION OF THE PLATES.

LETTERING.

d, first cleft in the mesoderm.
o, *i*, *j*, *k*, *l*, indicate respectively successive clefts in the mesoderm posterior to the first cleft, *d*.
f, *g*, position of first and second clefts anterior to *d*.
1–6, successive protovertebræ posterior to the first mesodermic cleft, *d*.
a, *b*, first and second protovertebræ anterior to the first cleft, *d*.
III., V., VII., VIII., IX., X., third, fifth, seventh, &c. cranial nerves.

A. Prosencephalon.
B. Thalamencephalon.
C. Mesencephalon.
D. Metencephalon.
E. Myelencephalon.
aud. auditory capsule.
ect. ectoderm.
h. heart.
inf. infundibulum.
m. p. muscle plate.
n. c. neural crest.
n. ch. notochord.
n. sp. spinal "neuromeres."
p. v. protovertebræ.
sp. g. spinal ganglion.
v. fourth ventricle.
x. section broken.

1′, 2′, 3′, 4′, 5′, neuromeres of the medulla.

PLATE I.

Sagittal sections, showing the development of the protovertebræ.

Fig. 1. The first mesodermic cleft is seen anterior to the first protovertebræ. × 60
Fig. 1 a. Same, enlarged. × 180.
Fig. 2. Section from an embryo with two protovertebræ, showing the peculiar shape of protovertebra *a*, which is due to the less rapid proliferation of cells in its anterior portion. × 330.

Fig. 3. Embryo with three protovertebræ. The shape of protovertebra *a* much the same as in the embryo of two protovertebræ. × 330.

Fig. 4. Section from a chick with four protovertebræ. × 180.

Fig. 5. " " " five " × 160.

Fig. 5 a. " " " five " × 160.

Fig. 6. " " " six " × 160.

Fig. 7. " " " seven " × 165.

Between *f* and *g* is seen the beginning of the protovertebra anterior to *a*.

Fig. 8. Sections from a chick with eight protovertebræ.

PLATE II.

Fig. 10. Horizontal section showing the origin of the V., VII., and VIII. cranial nerves in a chick with fifteen protovertebræ.

Figs. 11, 11 a. Two sections from the same series. Fig. 11 shows the origin of the IX. nerve from the neural crest back of the auditory capsule (*aud.*). Fig. 11 a is a more ventral section, showing the relation of the ear capsule to the neural concavity dorsal to which the IX. nerve arises. Horizontal sections.

Fig. 12. Shows the neuromeres between which the nerves arise, as indicated. Sagittal section.

Fig. 12 a. Sagittal section, showing the two roots of the VII. and VIII. cranial nerves.

Fig. 12 b represents the right medullary wall from a horizontal section, showing the cell arrangement of the neural ridges connected with the VII. and VIII. cranial nerves.

Figs. 13, 13 a. Sections from two 4½-day chicks. They show the relation of the spinal ganglia (*sp. g.*) to the muscle plates (*m. p.*), and to the neuromeres of the spinal cord (*n. sp.*). 13 a is sagittal; 13, horizontal.

Fig. 14. Median sagittal section, showing the relation of the five main divisions (A, B, C, &c.) of the brain, after the cranial flexure.

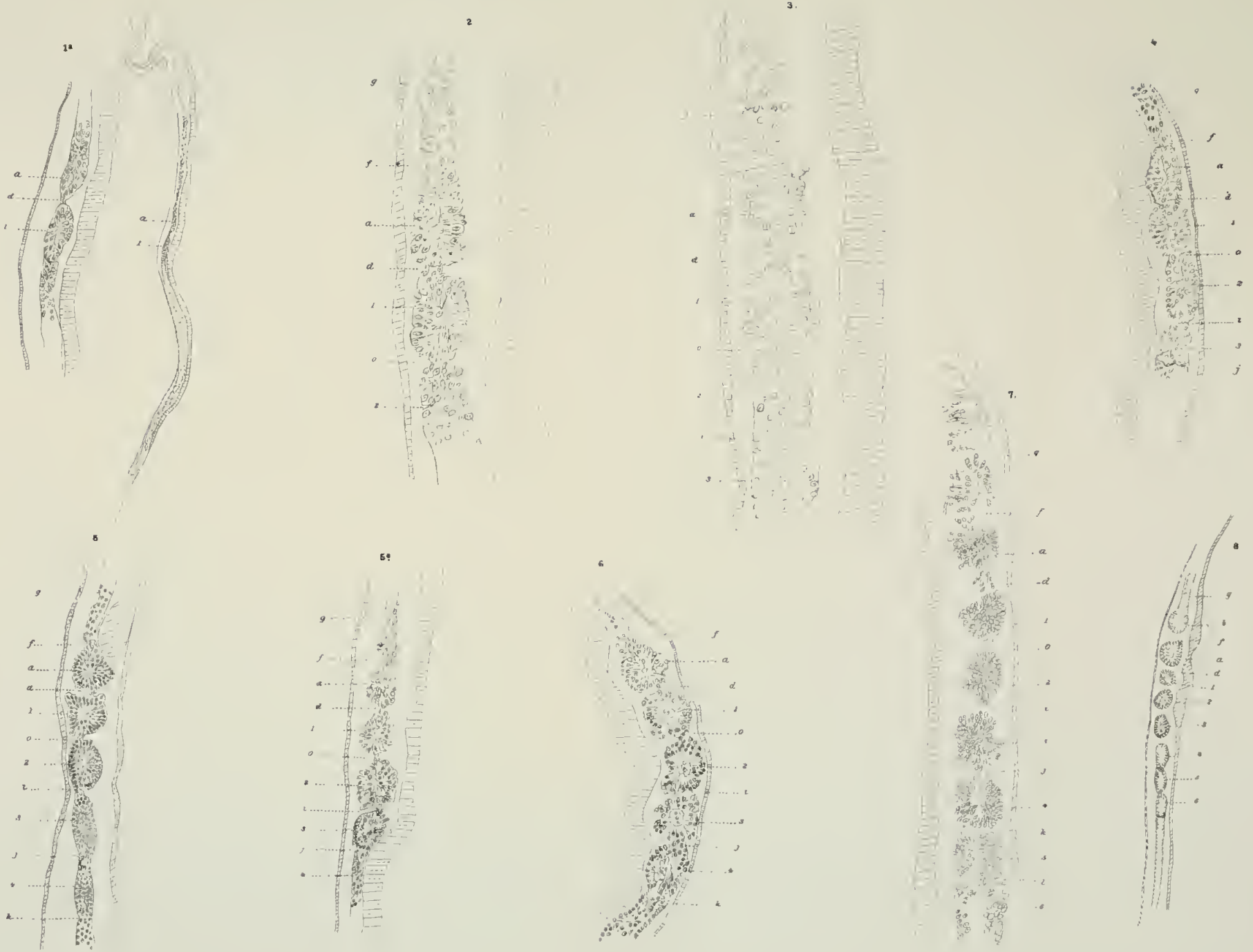
Fig. 15. Median sagittal section, showing their relations at the beginning of the cranial flexure.

Fig. 16 shows the neural ridges in the medulla of a five-day chick. The roof of the fourth ventricle and mid-brain have been removed.

Fig. 17. Diagrammatic representation of the relation of the successive cranial vesicles at the time of their first appearance.

Fig. 18. Sagittal section through the lateral wall of the medulla in a five-day chick. In hardening, the mesoderm has broken away from the neural wall.

Fig. 19. Sagittal section near the middle line of the brain of a four-day chick.


1a
2
3.
4
5
5a
6
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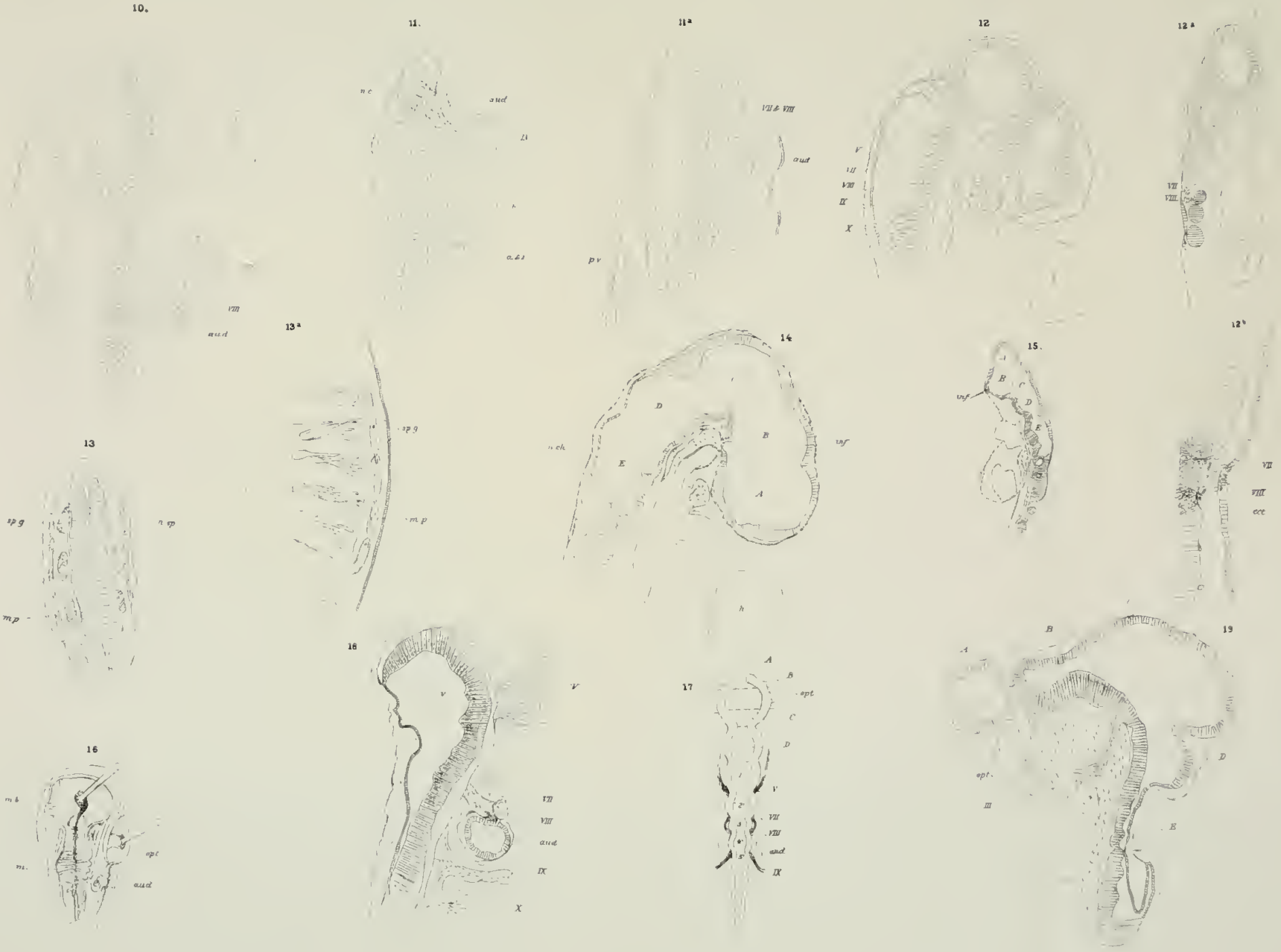
B Meisel, lith


10.
11.
11a
12
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No. 5. — *The Morphology of the Carotids, based on a Study of the Blood-vessels of Chlamydoselachus anguineus, Garman.* By H. Ayers.

Chlamydoselachus* holds undisputed claim to being the most lowly organized Elasmobranch yet discovered, and it was to have been expected that primitive conditions of organization would be retained to a greater extent than in any other known member of the group, the vascular system not excepted.

Almost nothing is known of the vascular system of the Notidanidæ, but it may be inferred from a comparison of their other structures with the corresponding organs in Chlamydoselachus that their vascular system will not be found to retain all the primitive characters present in Chlamydoselachus. This primitiveness of structure is expressed, 1st, in the retention of a large number of aortic arches; 2dly, in the presence of the complete dorsal aorta, of which the precardiac portion among the remaining vertebrates is almost without exception either extensively or completely atrophied; 3dly, in the extensive venous spaces, always simple in character, developed in the course of the large venous trunks.

While at the Banyuls-sur-Mer zoölogical station in the spring of 1885 I reached the conclusions, (*a*) that the vascular system of existing sharks had been extensively abbreviated in the course of descent in connection with the development of the head; (*b*) that formerly there must have been a much larger number of aortic arches than we now find in any member of the Elasmobranch group; and (*c*) that with the loss of the aortic arches the dorsal aorta of the branchial region had disappeared either entirely or in part. As examples of the latter condition

* The two papers containing the original descriptions of the systematic position and anatomical characters of *Chlamydoselachus anguineus* from the type in the Museum of Comparative Zoölogy at Cambridge, Mass., include all that is known of the creature: —

[1] Garman, Samuel. New Sharks, Chlamydoselachus anguineus, etc. Bull. Essex Institute, Vol. XVI. p. 1.

[2] The same, 1884. Chlamydoselachus anguineus, Garman. A Living Species of Cladodont Shark. Bull. Mus. Comp. Zoöl., Vol. XII. No. 1. Cambridge, Mass., 1885.

we have several species of sharks whose anatomy has been described by Hyrtl,[3] Parker,[4] and others, such as Scyllium, Mustelus, Zygæna, etc. Furthermore, it seemed to me that the accumulation of blood-vessels about the hypophysis cerebri could be reasonably accounted for on the assumption that the vessel which Hyrtl[3] describes is in truth a remnant of a much larger vessel of functional activity during embryonic life only, which sustained such relations to the vascular structures about the pituitary space as would lead us to search for the remains of preoral aortic arches. His words are as follows (*loc. cit.*, p. 5): "Bei feinen Injectionen lässt sicht leicht erkennen, dass diese Aorta, welche Kopfaorta genannt zu werden verdient, durch eine in die Mittellinie des Schädel-basalknorpels nach vorn gehende Fortsetzung bis zur Eintrittsstelle der Carotis interna in die Schädelkapsel sich erstreckt. Tab. I. Fig. 1, lit. i." Again the vessels called carotids by Hyrtl,[3, 5] Müller,[6] and Parker,[4, 7] seemed to complete the aortic circulation in front by bringing blood from the ventral to the dorsal side of the digestive tract, and were in a special sense the homologues of the carotids of the Mammalia, of which more will be said further on.

These conclusions were the outgrowth of my verification of Hyrtl's[3] descriptions and figures of the arterial blood-vessels of the head in Scyllium, Acanthias, and Mustelus. I did not at that time expect to be able to verify my conclusions by the dissection of any living animal, and consequently considered the views which form the essence of this paper to be of little value because not demonstrable. The vascular system of Chlamydoselachus proves the contrary, however, and under the circumstances it is now a matter of no inconsiderable interest to find out how the Notidanid sharks comport themselves with respect to the cephalic arteries.

I am not certain that Hyrtl has ever seen the "Kopfaorta" as it exists in Chlamydoselachus, (i. e. imbedded in the cartilage of the basis cranii,) for from his description of it quoted above it is not clear whether the injected vessel figured in his plate runs in, i. e. through, the basis cranii, or only in the middle line and ventrad of that structure.

[3] Hyrtl, Joseph. Die Kopfarterie der Haifische. Denkschrift. d. Wiener Akad., XXXII., 1872.

[4] Parker, T. J. On the Blood-vessels of Mustelus antarcticus. Phil. Trans., Vol. CLXXVII., 1886.

[5] Das Arterielle Gefasssystem der Rochen. Wiener Sitzungsberichte, 1857.

[6] Müller, Johannes. Vergleichende Anatomie der Myxinoiden. Berlin, 1839–41.

[7] Parker, T. J. Zoötomy, 1884.

At present I doubt not that Hyrtl found in every case only an extra-cranial vessel *so far as he traced it*, and that perhaps he did not follow it quite to its end on account of the non-penetration of the injection mass beyond the point of entrance into the cartilage.* While studying the same species at the Laboratoire Arago it did not occur to me to seek for the vessel within the substance of the cartilaginous brain case, and I always found the vessel very much as Hyrtl figures it, though usually I was not able to trace it so far anteriorly as it is drawn in his plate. Since my attention has been called to the matter I have dissected only one specimen of *Scyllium stellare* from the Museum alcohol collections, but the histological condition of the tissues did not permit a satisfactory determination of the relations of the vessel. Further study of this form is very desirable. So far as the homology of the two vessels is concerned, there can be no question that they have strictly the same morphological value.

To aid in understanding the relations of the carotids, and to serve in the comparison of other forms, as well as to give an idea of the fundamental simplicity of organization of the vascular system, I shall first describe the aortic system of blood-vessels in Chlamydoselachus passing thence to a consideration of the homologies in other vertebrates in so far as lies within the scope of this paper.

The sinu-auricular (see Figure 2) valve is placed in the middle of the transverse axis of the sinus venosus with its long axis at right angles to the axis of the latter. It is slit-like and guarded on either side by two broad semilunar tendinous folds, — the sinu-auricular valves. The remaining auricular wall of the sinus is smooth, muscular in some degree, but thin.

The aperture of the auriculo-ventricular valve is placed to the left, below and in front of the sinu-auricular valve, and pierces the thick ventricular wall. Its ventricular end is provided with two cup-shaped folds, the auriculo-ventricular valves. Its auricular end presents a radiate figure formed by the tendinous cords of the muscular plate, which centre here. The dorsal wall of the auricle is smooth without, but rugose within. It is scarcely thicker than the wall of the sinus venosus. The ventral wall of this division of the heart is thick and muscular, and forms a triangular plate which projects beyond the edges of the ventricle,

* Müller certainly did not see the vessel in any species studied by him, for he says (*loc. cit.*: "Bei den Haien u. Rochen fehlt die vordere umpaare Fortsetzung der Aorta schon ganz, wie bei den Knochenfischen aber die Haien besitzen noch einen circulus cephalicus im Sinne Hyrtl's," etc.

from which at about the middle it may be separated. This plate reaches cephalad to the middle of the conus arteriosus, but is not bound to it in any way.

The *conus arteriosus* (see Figure 2) forms a thick spindle-shaped trunk about an inch long and one fourth of an inch in diameter. It is provided with six rows of valves, all of which are quite small, except the anterior set of three, which are large, tridentate, and formed of a white tough tissue of a cartilaginous consistency. In Odontaspis the conus is bounded anteriorly by three large valves, each of which consists of two thin membranes united by a thick median bar which ends in a pointed projection beyond the anterior border of the valve.

The *pylangium* terminates anteriorly in a synangium or bulbus arteriosus, from which spring three vessels, one median and two lateral, the ventral aorta, and the sixth pair of afferent branchial arteries, respectively. The synangium is not so well developed in Chlamydoselachus as in Raja or most Elasmobranchs, for, while in the former a single pair of afferent branchial arteries arise from it, in the latter the common trunk known as the posterior innominate artery of the skate represents at least three primitive afferent branchial vessels, and in consequence the synangium represents a very much greater portion of the primitive ventral aorta in Raja than it does in Chlamydoselachus.

The synangium of Chlamydoselachus includes the enlarged end of the ventral aorta lying between the last pair of pylangial valves and the point of origin of the ventral aorta (in the restricted sense), and the sixth pair of afferent branchial arteries. It forms a truncated cone-shaped body, the homologue of the bulbus arteriosus of bony fishes. The ventral aorta continues the synangium forwards along the median line, and lies in a distinct sheath formed by the connective tissue separating the basibranchial cartilages from the muscles of the floor of the branchial basket. This sheath forms the outer wall of a lymph space.

The ventral aorta (see Figure 2) ends blindly in front in an anchor-shaped enlargement formed by the bifurcation of the median trunk and the separation of the two resulting vessels, — the anterior innominate arteries, — which curve outwards, upwards, and backwards, quickly splitting into two pairs of vessels the first and second afferent branchial arteries. From the anterior edges of the anterior innominate arteries, equidistant from the median line, arise two small vessels, which, passing forwards, supply the muscles in the ventral wall of the throat. Other small vascular twigs arise from the ventral aorta as well as the afferent branchial arteries to carry blood to the muscles of the ventral portion of

the branchial apparatus and to the heart. In the saurian Varanus, according to Wiedersheim,[8] (p. 704, Fig. 540, B,) it appears that a portion of the ventral aorta (or ventral commissures?) remains as a single median trunk, from which both the common carotids are given off just ventrad of the hyoidean apparatus, to rise on either side of the throat. The common carotid trunks thus occupy the position of the hyoidean efferent branchial vessels of the Elasmobranch. This common trunk divides above the level of the pharyngeal roof into an external and an internal branch. We thus see that in different animals the carotids have not the same value *in so far as their proximal ends are concerned.* The afferent branchial arteries (see Figure 2) number six pairs, and are arranged in sets of two pairs each. While the first two pairs of arteries arise from a common trunk, the arteries of the other pairs arise independently, with the members of each pair placed opposite each other.

The anterior innominate artery does not divide into first and second afferent branchial arteries until after it has curved upwards about a quarter of an inch, when the first afferent branchial springs from the anterior edge of the innominate and continues its trunk dorsad, curving gracefully forwards, outwards, and upwards, then considerably backwards to where it enters and supplies the anterior half of the first gill cleft, or the hyoidean demibranch. The second afferent branchial passes backwards at an acute angle from its origin at the posterior border of the root of the first, and in its outward and upward course nears the third afferent branchial where the latter enters its arch.

The sets composed of the afferent branchials three and four, and five and six, respectively, are so disposed that while five and six leave the synangial end of the ventral aorta, three and four arise from the middle of this trunk. There are slight variations in the size of the vessels forming the pairs two, four, and five, the arteries of the left side being larger than those of the right. The afferent branchials three, four, and five run very nearly parallel with one another, and while the efferent branchials of the pairs three and four continue this relation above the intestine, efferent branchial five bends suddenly backward and fuses with the sixth before entering the dorsal aorta.

There are six pairs of efferent branchial arteries (see Figs. 1 and 2), corresponding pair for pair with the afferent branchials just described. Only four pairs reach the median dorsal line to form the dorsal aorta; these are the second, third, fourth, and fifth. The first efferent branchial

[8] Wiedersheim, Robert. Lehrbuch der vergleichenden Anatomie der Wirbelthiere. Jena, 1886.

is connected by an anastomosing branch with the second, just as the latter emerges from its arch to enter the roof of the mouth, and thus at least a portion of the blood from the hyoidean demibranch reaches the dorsal aorta; but as the trunk of the first efferent branchial artery passes out of the hyoid arch it curves forwards along the outer edge of the basis cranii, and runs as far forwards as the middle of the orbital region, where it suddenly curves inwards to a point at one side of the median line, just below the pituitary space, the floor of which it perforates to enter the cranial cavity. This is the first impression produced on laying bare the vessels in Chlamydoselachus, but, as we shall see later on, all of this trunk lying beyond the upper end of the hyoid is foreign to the first efferent artery, whose continuation we are to seek in the branch uniting it with the second, and is simply the trunk of the common carotid artery.

The commissural branch uniting the hyoidean or first efferent branchial artery to the second is fully as large as the arteries themselves, and from its manner of union with the second and of its separation from the first efferent branchial makes the conclusion unavoidable that it is in truth the continuation of the trunk of the first efferent branchial, which however fails of an independent union with the dorsal aorta, but in a manner similar to that in which the homologous arteries in Scyllium, Acanthias, and Zygæna (Hyrtl, *loc. cit.*, Plates I.–III.) are united, i. e. by the fusion of the latter with the next succeeding branchial artery (see Figs. 10 and 11). This method of fusion is carried to an extreme in the bony fishes, where all the efferent branchials of each side unite to form the single pair of aortic roots (Müller, *loc. cit.*, Plate III. Fig. 13), and is also represented in Chlamydoselachus in the posterior section of the efferent branchial system by the fusion of the sixth and fifth efferent branchials to form a single aortic root. Under primitive conditions of the hyoidean gill this anastomotic vessel would take blood from the anterior demibranch of the hyoidean gill sac and the posterior demibranch of the mandibular gill sac, — holobranch of Parker. On account of the reduction which has taken place in the spiracular gill among existing Elasmobranchs, this vessel serves simply to convey the blood from the anterior demibranch of the first gill sac into the efferent artery of the first holobranch.

As in the afferent branchial system, so in the efferent branchial system, the component arteries are arranged in pairs, and the pairs correspond, though the paired condition is less marked in the efferent than in the afferent system.

The first and second efferent branchials unite to form a trunk that reaches the aorta as the second aortic root. The third and fourth pairs find independent outlets as the third and fourth aortic roots, while the fifth and sixth pairs fuse directly to produce short common trunks, the last or fifth pair of functional aortic roots.

The distance between the points at which the first and second and the second and third efferent branchials enter the aorta is nearly the same, while the common trunks of the fifth and sixth enter the aorta at a distance behind the fourth twice as great as that between the other pairs.

Unlike all other gnathostomous vertebrates, Chlamydoselachus has a dorsal aorta (dorsal vessel) running the entire length of the notochord, to which it is intimately attached through the greater part of its course. There is, however, no trace of a chondrification of its walls, such as frequently occurs in cartilaginous fishes (e. g. Sturio). For convenience in describing as well as on morphological grounds, it is desirable to designate two sections of the dorsal aorta by the terms *precardiac* and *postcardiac*. The former receives the aortic roots and supplies the head with arteries, the latter gives off the arteries to the trunk and tail.

The head and all the precardiac portion (see Figs. 1 and 2) of the trunk are supplied with blood by means of the very primitive musculo-spinal arteries and branches of functional or rudimentary aortic arches. This fact is of the greatest importance in any discussion of the homologies of the head arteries, or more exactly precardiac arteries, of the higher Vertebrata. These vessels where more or less rudimentary as regards their main trunks have undergone secondary changes, during which the course of the blood currents through them may have been reversed, and they have usually acquired new outlets, or inlets, as the case may be.

It is convenient to make a further division of the precardiac section into cranial, vertebral, and branchial portions. The precardiac section is marked off posteriorly by the junction of the fifth pair of aortic roots with the sub-chordal vessel. It terminates anteriorly in the pituitary plexus. The postcardiac section extends from the junction of the fifth pair of aortic roots to the tip of the tail. (See Figs. 1 and 2.) With the exception of a slight enlargement in the occipital region, the diameter of the aorta is constant between the occiput and the origin of the cœliac artery ; from this point backwards the aorta gradually tapers into the small caudal artery. From the occiput forwards the cranial section of the precardiac aorta lies imbedded in the cartilage of the basis

cranii; sinking into the cartilage just in front of the posterior border of the basi-occipital cartilage, it runs forwards, gradually rising to the inner surface of the cranial floor, remaining equidistant from the chorda until near the anterior end of the latter, when the aorta dips slightly to make a bold curve upwards into the pituitary prominence within which it gives off two lateral branches which separate from the median vessel only gradually. (See Figure 3.) These three vessels make their way through the cartilage, and by freely anastomosing with one another form a small but sharply defined plexus, crowning the pituitary prominence, but separated from the cartilage by several well defined layers of connective tissue, one of which bridges over the pituitary depression, and thus excludes the internal carotids from the cerebral cavity. The plexus lies external to the dura mater.

As we have seen, the aorta is made up by the confluence of six pairs of efferent branchial arteries, which pour their blood into the aorta through only *four* aortic roots, and in this condition we recognize the process of reduction, transposition, or utter obliteration at work in getting the creature out of a lower into a higher stage of organization. But the four aortic roots which bring blood from the gills are not the only trunks which from their relations to the aorta and the body make good their claim as aortic arches or roots. As Hyrtl has pointed out, the pair of vessels running from the internal carotid trunk to the aorta in all sharks is most surely an aortic arch, and although it has lost its direct connection with a gill, which we have every reason to believe it formerly had, it still retains its connections with a trunk which has resulted from the obliteration of *a series* of efferent branchial vessels, and through this trunk an indirect connection with the first two functional gills of Chlamydoselachus. Besides this pair, there is another whose relations to the dorsal aorta are such as to entitle them to rank as aortic arches. I refer to the two side branches which the dorsal aorta gives off as it approaches the pituitary plexus. To these six aortic arches I would add a pair represented by the anterior portion of the internal carotid arteries, and another pair represented by the efferent vessels of the spiracular pseudobranch, which pour their blood into the dorsal aorta through the ophthalmic artery, internal carotids, carotid plexus, and pituitary plexus, all of which vascular structures anastomose among themselves from without inwards, in the order given. To these still another pair may be added, recognizable in the last pair of efferent branchial arteries (the sixth functional pair), which by means of their fusion with the fifth pair have not been counted. Chlamydoselachus

has then, in all, nine aortic arches and remnants of arches, persisting from an earlier and more primitive condition of organization. This count is based on the demonstrations and suppositions, (*a*) that the anastomotic branch between the hyoidean demibranch and first efferent branchial is the continuation of the hyoidean efferent artery; (*b*) that the internal carotids after turning inwards and entering the pituitary space unite with the dorsal aorta; (*c*) that the anterior end of the cranial aorta divides, and that the lateral vessels curve outward each side of the anterior end of the notochord; (*d*) that the efferent artery of the spiracular pseudobranch is connected with the aorta; and (*e*) that the sixth efferent branchial artery formed at one time (probably during embryonic life) an independent aortic root. The fact should not be overlooked that we thus find remnants of two, and perhaps three, aortic arches *in the pituitary space!* (See table on page 218, and Figs. 1 and 2.) That the above method of counting the aortic arches in Chlamydoselachus is a correct one, within very narrow limits of error, no one will question who recognizes the vast changes that have been brought about in the vascular system of a higher vertebrate — mammal, for instance — during its phylogenetic course from the fish type upwards, and who recognizes the general law that an organism makes use of rudimentary or disused structures to build up other structures, of different function perhaps, for use under changed conditions of environment, provided the rudiment or disused structure be *suitably placed.* The only portions of the vascular apparatus of the branchial region that are suitably placed for use in case the aorta is reduced, are evidently the dorsal and ventral commissural systems. That the dorsal vessel should be chosen of the two is further evidence of the law, for the dorsal commissure is both more directly connected with the territory to be supplied, and lies deeper in the tissues in a direct line toward the brain; besides, it normally carries the purified blood from the gills, which the ventral commissures do not to so great an extent, lying as they do on the side of the gills where the currents are forming and setting towards the dorsal vessel. As a further illustration, we find in some species of Myxine the remnant of a ductus Botalli. This remnant was in early adult life hollow, and connected the gills of its half of the segment with the dorsal aorta. Müller found in some cases that each end of the thread-like remnant was still hollow. These threads arise from the afferent branchial artery of the anterior gill sac, passing thence upwards and forwards, and fuse with the carotid trunks where the latter anastomose with the first efferent branchial arteries. In

this instance the vessel is atrophied during the process of the reduction of the anterior gill, and the blood which formerly passed through it direct to the collecting vessel above its gill now passes backward, and its segment of the collecting vessel is now either carotid or carotid root.

Since the number of efferent branchial arteries uniting to form the dorsal aorta varies in different species, the dorsal aorta cannot be an equivalent structure throughout the vertebrate series.

We know that the cranium itself is not an equivalent structure within the limits of the Elasmobranchii. Abundant proof of this has been collected by Gegenbaur,[12] Froriep,[13] Van Wijhe,[14] Dohrn,[15] and others. Evidence based on the relation of blood-vessels to the cranial floor is worthy of note in this connection. In some Elasmobranchs the anterior pair of musculo-spinal arteries pierces the cranial floor, in other forms this pair is intimately related to the atlas. Where the former condition is present, we can say definitely that at least one vertebra has been added to the cranium, but in the latter case we may have to deal with a suppression of one or more pairs of musculo-spinal arteries, in which case we cannot draw conclusions as to the constitution of the cranium.*

Since there can be little doubt, if any, that the *primordial cranium* is the same in all cases, it follows that, during the early stages of ontogeny, segments (cranial vertebræ) must have been added to the occipital region in a large number of cases, and we are at once confronted with the difficulty of determining the number of such added segments, and

[12] Gegenbaur, C. Die Metamerie des Kopfes u. die Wirbeltheorie des Kopfskeletes. Morph. Jahrbuch, XIII., 1887.

[13] Froriep, A. Ueber ein Ganglion d. Hypoglossus u. Wirbelanlagen in d. Occipitalregion. Arch. f. Anat. u. Physiol., 1882.

[14] Van Wijhe, J. W. Ueber die Mesodermsegmente u. d. Entwickl. d. Nerven des Selachierkopfes. Konigl. Acad. d. Wissensch., 1882.

[15] Van Bemmelen, J. F. Ueber vermüthliche rudimentäre Kiemenspalten bei Elasmobranchiern. Mitt. d. zoolog. Stat. zu Neapel, VI., 1885.

[16] Dohrn, Alex. Studien zur Urgeschichte der Wirbelthierkörper. Mitt. d. zoolog. Stat. zu Neapel, VII., 1887.

* Transsections of the basis cranii of Chlamydoselachus taken from the vertebral junction forward show at intervals calcified tracts leaving the central perichordal crust, and extending on either side out into the hyaline cartilage. They correspond in position to the neural arches, transverse processes, and hypapophyses of the vertebræ. (See Figure 8.) It may be possible to determine the number of vertebræ entering into the basis cranii of Chlamydoselachus by making a perfect series of such sections and counting the number of these vertebral remains.

thereby the limits of the primordial cranium. It is apparent from Müller's studies, that the Myxinoids possess a typical and well developed system of aortic vessels, and that Petromyzon differs more in degree than in kind from the Myxinoid type, for the structural plan is undoubtedly the same in both. The views which have hitherto been held by morphologists of the nature of the aorta in Craniates do not permit us to establish a homology of parts between this group and Amphioxus, the only living representative of the Acraniates.

Examining first of all the vascular system of Amphioxus as the type from which we may expect the simplest exposition of the fundamental vertebrate plan of structure, we find that it resembles in many respects the annelid type. For our purpose now, it will be sufficient to describe its precardial and postcardial sections. We find that, while they are not distinctly separated, the former corresponds to the branchial and prebranchial systems of vessels, the latter to the dorsal aorta, its branches, and its complement, the ventral (subintestinal) vein. Of importance is the fact that there are at first *two* aortic arches, forming the anterior termination of the aortic vessels and in this case of the vascular system, one of which disappears later in life quite completely as an arch, but persists in part as an artery supplying the naso-facial region, and that these arches do not project to the anterior end of the notochord, — a condition that may or may not be a secondary one.

Langerhans[9] (*loc. cit.*, p. 337) describes the arches and dorsal aorta as follows: "Von der Arteria branchialis gehen zwar Gefässe unter dem Constrictor veli zum Mund. Dann aber setzt sich das Herz fort in einem sehr weiten rechts verlaufenden Aortenbogen, während es links keinen ähnlichen entsendet, sondern geschlossen ist. Dieser rechte Aortenbogen zieht hinter dem M. constrictor veli nach oben, liegt in seinem oberen Theil mit dem Muskel, zum Theil in derselben Querebene und verbindet sich mit der rechten Aorta, während die linke anscheinend in keine Beziehung zu ihm tritt. Der Theil der Aorta unmittelbar hinter der Einmündung des Aortenbogens in die rechte Aorta ist bei beiden gleich weit. Nach vorn aber setzt sich die linke Aorta bis zur Mundhöhle als schmales Gefäss fort. Rechts dagegen biegt der grosse sinuöse Aortenbogen, nachdem er sich mit der rechten Aorta verbunden, nach vorn um und erstreckt sich etwas unterhalb und seitlich von der Chorda gleichfalls bis zur Mitte der Mundhöhle nach vorn, um hier abgerundet zu enden."

[9] Langerhans, P. Zur Anatomie der Amphioxus lanceolatus. Arch. f. mikr. Anat., Bd. XII., 1876.

Hatschek's studies of the development of the organs of Amphioxus do not seem to have been extended to the vascular system, for he does not mention the blood-vessels in his paper.

Schneider[10] quotes Langerhans, and adds the following observations of interest. He says (*loc. cit.*, p. 26): "Am oberen Ende entspringt von jedem Kiemenstabe eine (Taf. XIV. Fig. 2 v. b.) Kiemenvene welche bogenförmig ein wenig nach rückwärts verläuft und sich mit der Aorta verbindet welche jederseits unter der Chorda liegt. Die Kiemenvenen sind sehr dünnhaütig, man kann sie nur sehen, wenn sie mit Blut erfüllt sind. Die Aorten der Kiemengegend zerfallen in zwei Theilen. Der untere Theil liegt in der Falte welche die obere Branchialrinne seitlich begränzt, ihr Querschnitt ist spitzwinkelig, der obere Theil liegt in dem Bindegewebe welches der Chordascheide nach unten aufliegt und welche zu dem Gallertgewebe gehört. Die Aorta ist in der Kiemengegend doppelt, hinter derselben wird sie einfach bis in das Schwanzende. . . . Von der Aorta gehen dreierlei Zweige ab. 1. Arterien nach oben für die Muskeln der Leibeswand; 2. Arterien an der Innenfläche der Bauchhöhle. 3. Capillaren für den Darm. Obgleich die Zweige der ersten und zweiten Gruppe in ihren Verlauf den Arterien höherer Thiere gleichen, lassen sich doch Muskeln an ihnen nicht wahrnehmen. Von der ersten Gruppe entspringt je ein Zweig in einem Myocomma ungefähr in der Mitte desselben. Man kann ihn nach oben verfolgen bis über die Mitte der Chorda am weitesten in Kopftheile (Taf. XIV. Fig. 1, Ao. rechts). Die zweite Gruppe, die Arterien der Bauchhöhlenwand, entspringen an jedem Ligament und laufen auf der Innenkante des Ligaments nach unten. . . . Die der Mitte sich immer näherende Fortsetzung der rechten Aorta sich bis in die Spitze des Kopfes verfolgen lässt. Die linke Aorta verhält sich unregelmässig, sie geht in verschiedenen Exemplaren verschieden weit. . . . Auch Queräste sind vorhanden, welche beide Aorten verbinden. Wenn die linke Aorta früh verschwindet, liefern diese Queräste der rechten Aorta alle die Zweige, welche sonst der linken ausgehen würden."

According to Johannes Müller, the aorta in Petromyzon bifurcates a short distance in front of the anterior pair of gill sacs, anterior to the point of origin of the common carotid trunks, the two diverging limbs communicating on either side with the right and left common carotid trunks respectively. But in Myxine the aorta is continued to the anterior end of the notochord, and in fact extends by means of short

[10] Schneider, A. Beiträge zur Vergl. Anatomie u. Entwick. d. Wirbelthiere. Breslau, 1879.

terminal branches (e. g. palato-nasal) to the anterior end of the body, and there is no distinct bifurcation, the vessel, on the other hand, being gradually reduced by the numerous lateral branches given off after its passage through the circulus cephalicus. The aorta in Myxine is a relatively large vessel until it unites with, or, better, receives the two converging branches of the circulus, when it suddenly contracts, and from this point on is clearly much reduced. This portion of the canal still serves to keep open a direct passageway from the heart to the head, inasmuch as the arterial blood collected from the gills is not only forced upwards and backwards, but also forwards, into the continua tion of the aorta, or A. vertebralis impar, and into the carotid arteries.

I think, from the evidence gathered in the foregoing paragraphs, that we are now in position to say definitely that between Amphioxus and the Myxinoids on the one hand, and Chlamydoselachus as a representative of the Elasmobranchii on the other, it is easy to establish a homology of parts surprising in its completeness. The entire dorsal aorta exists in Chlamydoselachus, imbedded in part, it is true, in the basis cranii, while in Myxine it lies in the connective tissue underneath the latter. The long ventral aorta in these two forms has been much shortened, but still *in showing traces* of its reduction claims a descent from an Amphioxus-like type. Of course we should not expect to find the ventral aorta persisting after the gills in front of it had ceased to be functional, and it might easily shorten before such reduction of the branchial apparatus had taken place, provided means were at hand to enable it to perform its function of pouring blood into the gills. The dorsal aorta, on the other hand, being a distributing trunk in a large sense, would be looked for so long as its territory existed and was not entirely supplied by new vessels; and as we know that its territory persists in all vertebrates, and greatly increases in extent among the higher forms, the latter alternative is the only one we need consider further. We find, on examination, that the recession of the heart is accompanied by the usurpation of the precardiac aortic territory by some of its lateral branches or their smaller offspring. While it is true in general that a reduction of the ventral aorta is followed by a reduction of the dorsal vessel, it is also true that the latter process takes place much more slowly, and for the reasons given above. The only indication of a persistence of the dorsal aorta in groups above the fishes, of which I have been able to find reliable account, is given by Goette.[11]

[11] Goette, Alex. Entwickelungsgeschichte der Unke. Leipzig, 1875.

His figures on Taf. XVII. Figs. 306, 317, and 316 *a*, *c*, of frontal sections from embryos of *Bombinator igneus* show that the aortic roots anastomose by means of transverse vessels, and that at an early stage of development there is an anterior (median) prolongation of the dorsal aorta between and beyond the aortic roots! How long this remnant persists is not stated by the author.

A series of transsections (see Figs. 5 *a* to 5 *g*) through the basis cranii of Chlamydoselachus in the regions designated below as **1, 2,** and **3** (see Figure 1) gave the relations of the chorda and aorta to each other shown in the following table. The distances refer to measurements in the perpendicular to the long axis of the animal. The sections were taken from three portions of the basis cranii containing the structures cut from the vertebral junction, middle distance, and the pituitary region respectively, the last piece containing the whole of the "Sattellehne" and the pituitary space, with the foramina of entrance of the carotid arteries and the transverse canal.

TABLE OF RELATIONS OF CHORDA AND AORTA.

(*c* = chorda. *a* = aorta.)

(**1**) From the vertebral junction.

Section No. 1 { *c* in middle of section. / *a* below and entirely outside basis cranii.

" " 2 { *c*, the same as No. 1. / *a*, " " "

" " 3 { *c* in middle of section. / *a* inside cartillage, but on lower boundary.

" " 4 { *c* in upper half. / *a* in middle of lower quarter.

" " 5 { *c* in upper half. / *a* in middle of lower half.

" " 6 { *c* in upper half. / *a* in upper quarter of lower half.

(**2**) From this point on, the rise of the aorta is very gradual until the section from middle distance between occipital region and pituitary space is reached, when in

Section No. 1′ { *c* in upper third of section. / *a* in the middle of section.

" " 2′ { *c* in upper quarter of upper half. / *a* in middle of section.

" " 3′ { *c*, the same as No. 2′. / *a*, " " "

" " 4′ { *c*, " " " / *a*, " " "

Section No. 5′ { *c* in upper quarter.
a in the middle third but above the middle.

From the middle region the chorda and aorta both rise until each breaks through the surface of the cartilage, the chorda to end in the calcareous incrustation of the cartilage, and the aorta to enter the pituitary space from the summit of the saddleback. Two sections from region (3) gave in

Section No. 1″ { *c* on the upper surface of cartilage.
a in upper quarter of upper half.

" " 2″ { *c* section in front of chorda end.
a emerges from top of saddleback.

It will be seen from this table that the chorda occupies in the occipital region the middle of the cartilaginous plate of the cranial floor, and that from the end of the cone-shaped body, which was in the individual dissected about 1 cm. long, the thread remnant rises gradually but continuously until it reaches the inner surface of the floor of the cranium. This point, as the sections show, was *behind* the apex of the pituitary eminence (Sattellehne). Further, we find that the course of the aorta remnant is very nearly parallel with that of the chorda, and that it issues from the apex of the pituitary eminence in exactly the manner described by Gegenbaur for the chorda of other Elasmobranchs.

Gegenbaur [17] has investigated the subject of the chorda termination very thoroughly, and judging from the text and plates mostly by means of longitudinal section. There are several figures of cross sections of the basis cranii, showing the structure which he calls "Chorda," but which resembles the more ventrally placed aorta as I find it in Chlamydoselachus. As the author says, it is almost always a very difficult matter to determine the exact position and manner of the chorda termination in adult animals; much easier with young animals or older embryos. The author studied, among others, the genera Acanthias, Heptanchus, and Centrophorus. He says (*loc. cit.*, p. 121): "Die Chorda tritt mit ihrer Aufwärtskrümmung immer näher an die innenflache der Schädelbasis und steigt dabei in der Sattellehne empor, welche sie dicht unter deren hinterer Fläche durchsetzt, um nähe an der Kante dieses Vorsprunges unter das Perichondrium zu treten. Wo die Sattellehne starke corticale Verkalkungen zeigt ist das zugespitzte Ende der Chorda noch in diese eingebetet. Fig. 7, Taf. XIV. gibt eine Darstellung dieses Verhaltens in einem 22 cm. langen Acanthias Embryo auf dem Medianschnitte. Beim ausgewachsenen

[17] Gegenbaur, C. Das Kopfskelet der Selachier. Leipzig, 1872.

Thiere ist derselbe Zustand vorhanden, doch ist die Chorda im Vergleiche zum Basalknorpel bedeutend schwächer und die erweiterte Stelle ist nur angedeutet. Das hervortreten des Chorda-Endes aus dem Basalknorpel und die Lagerung unter dem bezuglichen Perichondrium hat Kölliker bereits gesehen, jedoch nicht der sehr auffälligen Beziehung zur Sattellehne sondern nur der Gegend der vor der Sattellehne gelagerten Hypophysis Erwähnung gethan: *In einigen Fällen sah ich das aus dem Knorpel der Sattellehne hervortretende freie Ende der Chorda* über die Kante der Sattellehne nach vorn umgebogenen aber immer noch unter dem Perichondrium verlaufend. So einmal bei einem 24 cm. langen Embryo von Acanthias, aber auch bei einem grossen Exemplare von Centrophorus granulosus. *Obgleich ich noch vier Acanthias-Embryonen darauf untersuchte, gelang es mir nicht, ein jenem ähnliches Verhalten verbreitert zu finden.*"

In the genera Heptanchus, Hexanchus, Centrophorus, Acanthias, Squatina, and Cestracion, the author traced the chorda dorsalis through the basis cranii to the saddleback (Sattellehne) of the pituitary depression, and found that the chorda remnant as regards shape, size, and position was very much alike in Hexanchus and Heptanchus. This remnant was in the form of an elongated conical body projecting into the occipital region of the basis cranii, forming of course the anterior continuation of the chorda in the vertebral column. From the apex of the cone was given off a pale thread of considerable size, which ran forwards usually parallel to the outer surface of the floor of the cranium. The arch formed in approaching the pituitary space is much weaker in Heptanchus than in Hexanchus. In Cestracion behind the pituitary saddleback the chorda swells out into a spindle-shaped body, whose fibrous sheath is filled with a cartilaginous tissue, containing numerous round hyaline cells. The structure of this spindle-shaped body, so far as Gegenbaur's description goes, agrees with that of the ventrally placed aorta in Chlamydoselachus, and not with the chorda, though it does agree with the chorda and its tubular enclosure in a very large (10 ft.) individual of Heptabranchias.

With reference to the persistence of the chorda in the cranial floor, Gegenbaur says (*loc. cit.*, p. 122): "Mit dem Nachweise der Fortdauer eines Theiles der Chorda dorsalis im Cranium mancher Selachier ist für diese ein niederstehendes Verhältniss aufgedeckt, nämlich die Fortsetzung eines bei den meisten Abtheilungen der übrigen Vertebraten bekannten embryonalen und damit vergänglichen Zustandes, der von den ihn daurend besitzenden Formen her sich ableiten lässt. Aus jenen Ver-

halten ergibt sich jedoch noch ein anderes bedeutungsvolleren Moment, jenes, nämlich, welche den von der Chorda durchsetzten Abschnitt des Craniums in gleichen oder doch zunächst ähnlichen Beziehungen zeigt, wie sie die Wirbelsäule zur Chorda besitzt, so das darauf eine Vergleichung jenes Abschnittes des Craniums mit einem Abschnitte der Wirbelsäule sich stützen kann." And further, "Aus der vollen Würdigung dieser Beziehung von Gehirn und Nerven des hinteren Abschnittes ergibt sich der offene Gegensatz zum Vorderen Schädelraum, der von dem hinteren sehr verschiedene Gehirntheile umschliesst und ebenso in den ihn verlassenden Nerven keinerlei Gemeinsamkeit mit den von Spinalnerven ableitbaren hinteren Nerven wahrnehmen lässt. Die Resultate der Vergleichung der einzelnen Abschnitte des Binnenraumes am ausgebildeten Cranium sind somit mit der Prüfung der Sonderungsvorgänge bei der Entstehung des Knorpelcraniums im Einklange."

To which if we add the weight of evidence afforded by the study of the vascular arrangements described in a previous paragraph, we have increased reason for the separation of the prechordal from the chordal section of the cranium. *For with this addition there is not a single important structure entering into the composition of the head which does not show traces of the originally distinct separation of these regions, now so closely united among all the higher vertebrates.*

Important in this connection is the relation of the chorda in *Bombinator igneus* figured by Goette, *loc. cit.*, Taf. IX. Figs. 164, 165, and 166, Taf. XV. Figs. 283 and 284, in which the author found the chorda dorsalis lying *below* the cartilaginous cranium, although in intimate contact with it. After its degradation, which takes place in an early stage of development, this portion of the chorda is converted into a (keel-shaped ?) calcareous crust, projecting from the ventral surface of the cranium. It is evident that in such a case the dorsal aorta could not become enclosed in the cartilaginous cranium, and in this fact we may have an explanation why a remnant of the aorta is not more uniformly found among the Elasmobranchs in general. It is important to bear in mind the condition of the head region before the cartilaginous cranium has been formed. In such a primitive animal, or at a corresponding stage in a more advanced form, the notochord, dorsal (and possibly ventral) aorta, digestive tract, and nervous cord extend through the head region, all parallel to the long axis of the body, and held in place by the connective tissue lying between them and whatever muscular and skeletal structures may be present. Branches from the nervous axis or the aorta easily find their way through the yielding tissue

to their destination.* So long as the intervening spaces remain filled with loose connective tissue, all these spaces are eminently vascular and lymphatic. The need of greater strength and power of resistance in the skeletal axis calls for a solidification in and about the notochord, and upon the extent of the hardened area depends the nature of the enclosures. Usually, of course, the notochord forms the centre of the solidified tract, but we have just seen that it may lie on the ventral border of this tract. The structures transverse to the axis are partly enclosed in the solidified tissue, — the proximal portions in the case of the nerves, the proximal or distal in that of the blood and lymph vessels.†

The question of the homology of the carotid arteries has been touched upon by many morphologists, and although the subject has never attracted any very great attention, several explanations have been proposed at various times. The usual one found in our text-books on comparative anatomy and embryology was the result of determinations made by the earlier embryologists, Bischoff, Rathke, and others, of the ontogeny of the vascular system in mammalian and other embryos.

Kolliker's [18] account contains the whole matter in clear and concise form, and I shall quote his words as a statement of the generally accepted views. He says (*loc. cit.*, p. 915): "Die erste Form derselben (i. e. die Arterien) die gleich nach der Entstehung des Herzens und während der Dauer des Kreislaufes im Fruchthofe getroffen wird, ist die (Fig. 560. 1) dass das Herz vorn einen Truncus arteriosus entsendet der nach kurzen verlaufe in zwei Arcus Aortæ sich spaltet, die in der Wand des Kopfdarmhöhle bogenförmig nach der Gegend der späteren Schädelbasis und dann längs dieser convergirend nach hinten laufen, um anfänglich getrennt von einander als doppelte Aorta descendentes zu enden und später unter einander zu unpaaren Aorta zu verschmelzen. Sowie die Kiemenbogen . . . hervortreten, zeigt sich, dass der Anfang der Aortenbogen in den ersten Kiemenbogen liegt, sowie dass auch für die folgenden Kiemen-

* These are the cranial and spinal nerves, the afferent and efferent branchials, and musculo-spinal arteries for the most part, all of which do not run parallel to the long axis.

† The blood-vessels are affected most by this process, and all except the important trunks rapidly atrophy, leaving as a last trace a fibrous cord imbedded in the solid cartilage.

[18] Kolliker, A. Entwick. des Menschen, etc. Leipzig, 1879.

[19] Rathke, H. Entwickelungsgeschichte der Natter. Königsberg, 1839.

[20] Rathke. Ueber die Entwickelung der Arterien welche bei Saugethieren von den Bogen der Aorta ausgehen. Arch. für Anat. und Physiol., 1843.

[21] Rathke. Entwickelungsgeschichte der Wirbelthiere. Leipzig, 1861.

bogen neue Aortenbogen hervortreten. . . . Die bleibenden grosse Arterien gehen im wesentlichen aus den drei letzten Aortenbogen hervor, *doch erhält sich auch ein Theil des ersten und zweiten Bogens in der Carotis interna und externa.*

"Von den drei letzten bogen wird der vorderste (der dritte der ganzen Reihe) zum Anfang der Carotis interna, während der Carotis communis aus dem Anfange des ursprünglichen ersten Arcus Aortæ sich entwickelt. Von der Aorta thoracica und abdominalis hat Remak zuerst gezeigt das dieselbe beim Hühnersembryo anfänglich doppelt sind, indem die ersten Aortenbogen nicht vereinen sondern als sogenante 'primitive Aorten' von der Wirbelsäule einander parallel bis zum hinteren Leibesende förtgehen. . . . Erst am dritten Tage verschmelzen diese 'primitiven Aorten' in ihren vordersten an der Wirbelsäule gelegenen Theile. . . . Hier sind die längstbekannten Arteriae vertebrales posteriores nichts anders als die 'primitiven Aorten' und stellen zahlreiche Figuren dieses werkes dieselben als paarige Gefasse am Kopfe und am Rumpfe dar. Die Verschmelzung dieser Gefasse . . . schreitet nach hinten fort."

Important points in this consideration are (*a*) the double condition of the aorta in the developing mammal; and (*b*) the persistence of portions of the first and second aortic arches in the carotid arches.

More recently Macalister [22] has offered an explanation of the carotid arteries which does not harmonize with the facts as I find them, and I shall first quote his remarks, and then show wherein it appears that his conclusions are not tenable in the light of the comparative anatomy of the lower fish forms. He says (*loc. cit.*, p. 193): "The arrangement of the blood-vessels in the adult forms of the lowest, and in the embryos of the higher vertebrates, indicates that the history of the complicated vascular system of the higher forms has been one of a development from a simple and regular ancestral condition of metameric and intermetameric vessels, through easily defined stages, to the more confused and irregular condition of the arterial system in the adults of the higher forms. . . . In the whole organism the vessels would thus form a double series, two longitudinal ventral trunks, two corresponding dorsal trunks, and the lateral uniting trunks in each segment. There are two primitive dorsal vessels in vertebrate embryos, and their fusion can be traced in the chick beginning at the forty-second hour of incubation. This union commences behind the head, and travels backwards rapidly,

[22] Macalister. The Morphology of the Arterial System in Man. Journ. Anat. and Physiol., XX., 1886.

so that after the fifth day there is but a single dorsal vessel for the middle and the hinder part of the body, — the dorsal aorta. In the region of the head and neck of mammals, *the foremost ends of the two vessels remain permanently separate as the internal carotid arteries.* [Italics mine.] . . . There were also originally two ventral longitudinal vessels, but their union probably occurred even earlier than that of the dorsal. . . . The setting apart of one portion of the single ventral vessel to form the heart differentiates the pre- from the post-cardiac portions of the ventral vessel. As a consequence of the cardiac differentiation, the only places where complete metameric arcades remain are the precardiac segments. . . . Behind the heart in higher vertebrates a series of vessels extend from the dorsal aorta through the mesogastric fold, and end in the splanchnopleure ; these correspond to the dorsal extremities of the postcardia lateral metameric arcades. With the condensation of the anterior segments which takes place in the formation of the skull, all distinct vascular metamerism is lost, and the anterior segmental arches become displaced backward or lost. The common and external carotids are continuations of the ventral aorta, while the root of the internal carotid is the altered relic of the third arch, and the ascending continuation of that vessel is the upper part of the dorsal aorta. . . . The only carotid branches which in any way represent rudimental arcades are the occipital and posterior auricular arteries. . . . The cervical dorsal aorta (internal carotid) has only rudimental branches in the neck, represented by the intercarotid ramuli. Its intracranial continuation gives off three lateral neural branches, the posterior, middle, and anterior cerebrals (the first originally being a carotid branch, its root being the so called posterior communicating, but its anastomotic internal branch, which joins the median anastomosis, dilates so as to form its functional root). The ventro-lateral branches are reduced and modified as tympanic, vidian, receptacular, and ophthalmic branches."

As the foregoing quotations show, Macalister tacitly assumes that the double nature of the dorsal vessel in mammalian embryos is comparable with that of some vermian type. He claims that the anterior ends of the double dorsal vessel are transformed into the internal carotid arteries of the adult, which is certainly true, but not in the sense our author intends it, as appears from the context, for he says further on, that the root of the internal carotid is the altered relic of the third arch. These views were, I believe, first expressed by Allen Thompson [26, 27] in 1831,

[26] Thompson, Allen. The Development of the Vascular System. New Phil. Journ., Edinburgh, 1831.

[27] The same. Quain's Anat., 9th ed., II., 1882.

who also claims to have discovered the facts on which they were based. Surprising is the statement that the external carotids are the continuations of the ends of the anterior bifurcation of the ventral aorta.

It is not possible at the present time to prove beyond doubt that the ancestor of vertebrates possessed only a single dorsal vessel; but the best evidence at the present time (the anatomy and development of the higher worms, and of those vertebrates retaining most of the ancestral features) points to an ancestral form having a single median dorsal vessel.

The embryological evidence cited by Macalister in support of his views, is interpreted by Balfour, Gegenbaur, Kolliker, Hertwig, and others, to be the effect of the shortening of the period of development, the suppression of some of the stages and the adaptation to peculiar embryonic environment.

In passing over the intermediate stages between the fish and mammal, our author has lost sight of the homologies of the vessels he deals with, and, so far as his account runs, has not seen the precardiac aorta in any vertebrate, but considers the two common carotid trunks to represent the pair of aortæ which his theory calls for.

The evidence which I have presented in the preceding pages shows beyond question that the carotid arteries, instead of being derived from the aorta or any of its branches, are derived from the commissures which serve to connect the efferent branchial arteries with one another. The bifurcated end of the aorta in the bird and mammal is only a remnant of a previous complicated vascular apparatus. It is likewise obvious that the carotid vessels cannot strictly be said to arise from, or constitute the remains of, any particular pair of aortic arches, but represent all that is left of the commissural trunk from the most anterior arch of the ancestral form to the most anterior arch of any given existing form.

About the time Macalister's paper on the homology of the blood-vessels of man appeared in England, T. J. Parker, working in New Zealand, published a paper in the Philosophical Transactions on the vascular system of *Mustelus antarcticus*, in which he advances decidedly interesting views as to the homology of the carotids of this southern shark. In the first place, Parker proposes to establish the terminology of these vessels on a scientific basis, and as the result of his studies objects to the use of the terms "internal" and "external" to designate the anatomical relations of the carotids as really misleading. He would substitute and use exclusively throughout vertebrates the terms "anterior" and "pos-

terior,"* as correctly describing the morphological relations of the vessels. Now, in as far as the terms are applied to the carotid arteries of the higher vertebrates as *names simply*, it matters little which set is used; but when it is proposed to select terms that shall harmonize with the development of the vessels † under consideration, *superior* and *inferior* are undoubtedly the correct ones, or dorsal and ventral.

In the light of Chlamydoselachus we may reasonably choose to retain the terms internal and external as describing at the same time the primitive condition of the vessels in the lowest vertebrates, and, when we consider the relations of the vessels to their territory of distribution (their only *constant* relation), and not alone their origin (in the anatomical sense) and source of supply (their constantly *varying* relation), also their anatomical relations up to and including man. The vessels are really never anterior and posterior so far as their points of origin are concerned, and this, as I understand it, is the basis of Parker's determination. As shown above, in primitive forms (e. g. Amphioxus and Myxine), the region supplied by the internal carotids in Acraniates and Craniates is provided for by branches from the superior portion of the curve of the first pair of aortic arches. The carotids arise from the dorsal prolongations of the aortic roots; i. e. from the tract homologous with the superior commissures of Elasmobranchs, and not, as Macalister and others suppose, the anterior ends of the two lateral aortæ on the one hand, or the corresponding parts of the ventral aortæ on the other. The carotid arteries are, in a strict sense, separated from the aorta by the vessel crossing the space between the dorsal end of the gill and the aorta which lies in the middle line. This vessel is equal to the dorsal portions of the efferent branchial arteries (or the entire epibranchials of Parker). It is because the inferior commissures are merely passageways for the transmission of blood to the distributing vessels in the dorsal region of demand, that they do not persist, since their function is early assumed by other vessels. As the aorta is gradually reduced by the backward journeying of the heart consequent on the reduction of the branchial vessels and organs, the brain and the enclosing head are removed farther and farther from the aortic arches from which they originally received their blood supply direct, by means of

* Parker's A. carot. post. = Art. carot. int.
" " ant. = eff. br. art. of mandibular gill, and *both* these vessels supply the region of the external carotid in sharks.

† Cf. Rathke (20) or Balfour (24). Comp. Embryol., II., 1881. I refer here to the development in the higher vertebrates.

numerous small twigs, and the aortic roots plus the superior commissures increase in importance with the retreat of the heart. In the Mammalia, where the aortic roots are reduced to the greatest extent, there is a very great variety in the manner of origin of the carotids from the aorta, or, in other words, the primitive relation of the carotid trunks to the median aorta has undergone a variety of transformations that for the most part are characteristic of the groups in which they are found. They remain as a pair of lateral longitudinal vessels, each of which almost universally divides into two branches, a dorsal and a ventral. The dorsal supplies the structures contained in the cranium, and gives off vessels into the orbital space; it is the internal carotid. The ventral branch supplies the visceral portion of the head and the cranial parietes, at least in part; it is the external carotid artery. The external carotid is then only a ventral branch of the dorsal commissural trunk, while the internal carotid continues the main stem of the common carotid. Of course, the relative sizes of the vessels undergo ceaseless variations as we ascend the series; but the rule is, that the higher the position of the animal in the series, the more important relatively the territory supplied by the external carotid becomes. For example, in man the two vessels, internal and external, are of about the same size; in the cat, the internal is small and the external correspondingly large. The two vessels may be united into a common trunk, and always are when the aortic arch from which they arise is much reduced, or they may arise independently of one another, as in Myxine. So long as the dorsal aorta persists entire, the carotids have no existence; but just in proportion as the precardiac section of the aorta is reduced, the carotid arteries become more and more important, until they ultimately entirely replace it, as in the vertebrates above the lower fishes. In Myxine, "Aus dem Zusammenfluss der Kiemenvenenstämme entstehen vier Hauptarterienstämme für den Körper, ein vorderer und hinterer unpaarer mittelerer, welche unter der Wirbelsäule hingehen, und zwei seitliche vordere. Die vorderen Theile des Körpers besitzen also zwei Carotiden und eine unpaare Wirbelarterie [i. e. precardiac Aorta] die hintern Theile des Korpers einen einzigen Arterienstamm, die Aorta descendens. Die Kiemenvenen der zwei oder drei letzten Kiemen gehen direct in die nach vorn und unten gleich sich verlängernde Aorta. Die Kiemenvenen der ersten oder zwei ersten Kiemen gehen nicht mehr in die Aorta über, sondern vereinigen sich jederseits in eine der Aorta parallele vena branchialis communis, welche sich nach vorn als Carotide fortsetzt. Die directe Fortsetzung der Aorta nach vorn, verlauft als arteria vertebralis

impar dicht unter der Chorda und versieht die Seitenmuskeln, das Rückgrath und Rückenmark mit zweigen. Die Carotiden begleiten die Speiseröhre und geben, ihren Seiten angewachsen, Zweige an sie ab. Hinter dem Kopf theilen sich die Carotiden in zwei Aeste welche eine Carotis externa und interna auf jeder Seite entsprechen. Die äusseren Carotiden vertheilen sich in dem Kopfmuskeln und in der Lunge. Die beiden inneren Carotiden verbinden sich bogenförmig unter dem Anfang des Rückgraths. Aus diesem bogen; der auch von hinten das ganz dünn gewordene Ende der unpaaren Wirbelarterie aufnimmt, entsteht nach vorn ein unpaarer starker Stamm. Dieser stellt gleichsam eine unpaare Wirbelarterie des Kopfes dar, er verläuft unter der Wirbelsäule über dem Schlund nach vorn, dann unter der Basis des Hinterschädels und senkt sich, da wo der Basis häutig wird, in der Mitte in die Tiefe, wahrscheinlich die Hirnarterien abgebend, indem er zugleich an dieser Stelle gabelig zwei dünnere Aeste ausschicht, welche divirgirend zur Seite des Nasengaumenganges neben den Knorpeligen seitlichen Gaumenleisten nach vorn weitergehen und dadurch in den Stand gesetzt werden wahrscheinlich den Nasensack mit Zweigen zu versehen."

The cephalic circle is complete in only a few forms (Myxinoids, Petromyzon, and the lowest Elasmobranchs). Among the Rays, Sturgeon (and all cartilaginous Ganoids?), and Chimæra, it is incomplete in front. But in *every* vertebrate except Amphioxus the internal carotids have their ends united by anastomosis within the *pituitary space* (Figures 14 and 4 *b*) usually, but always in this cranial region.

Referring to the anastomotic branch between the hyoidean efferent artery and that from the first branchial arch, Parker suggests that the union thus brought about is entirely a secondary condition, and that the true efferent trunk of the hyoidean gill is to be sought in the posterior (internal) carotid artery. He says (p. 690): "From the above considerations, one is led to look upon the connection of the first (hyoidean) efferent artery with the first epibranchial artery as a secondary one, and it then becomes a matter of considerable interest to find in *Mustelus antarcticus* distinct remains of the dorsal portion of the hyoidean aortic arch, and of its connection with the dorsal aorta. From the dorsal end of the first efferent branchial artery arises a large vessel, the posterior carotid artery. This trunk passes forwards and inwards ventrad of the proximal end of the hyomandibular, to the ventral surface of the auditory capsule, and through a foramen in the skull floor to the orbit. Its further course will be described hereafter; the point of interest for the present purpose is, that shortly before entering

the foramen just mentioned [see Fig. 12] at the point *x* in Fig. 12, it gives off a very slender vessel, *y*, which passes backwards and inwards along the ventral aspect of the skull and vertebral column, and joins with its fellow of the opposite side to form a delicate longitudinal median trunk, *z*, which is continued backwards to the junction of the first pair of epibranchial arteries. I think that there can be no doubt that the posterior carotid artery, from its origin to the point *x*, together with its backward continuation, *y*, represents the dorsal portion of the hyoidean aortic arch, or hyoidean epibranchial artery, the altered direction of the vessel being accounted for by the changed position of the hyoid arch. The middle trunk, *z*, is as obviously the actual anterior portion of what may be called the interhyoidean section of the dorsal aorta. It has clearly nothing to do with the arteria vertebralis impar of Myxinoids, which it resembles at first sight, since the latter is a secondary forward prolongation of the aorta altogether cephalad of the gills. As this anterior portion of the dorsal aorta undergoes complete atrophy — if indeed it ever exists — in the Rays as well as in the Holocephali, it is a matter of some interest to find it persisting in a typical Selachian, and one is led to inquire whether it is actually absent in those two forms the arteries of which have been described, or whether it has hitherto been overlooked. I can only say that I have failed to find any mention of it." Parker does not give the title of Hyrtl's [3] important paper in his list of literature, and makes no reference to it anywhere in his text. Presumably, then, he had at least no knowledge of its contents, or he would certainly have greatly modified the paragraph just quoted. In Chlamydoselachus, the arteries described by Parker for Mustelus are present as a strong pair of vessels diverging from the anterior end of the vertebral portion of the precardiac aorta, curving outward until they reach the internal carotid trunk, into which they open, some distance behind the internal carotid foramina. The fusion takes place even before the internal carotids begin to curve inwards toward the median line. Parker's conclusion, that the posterior carotid to the point *x* and the small vessel *y* form the hyoidean epibranchial artery is clearly untenable when applied to the more primitive Chlamydoselachus.

Parker's argument, that the unpaired aorta formed by the confluence of the vessels *y* is not comparable with the arteria vertebralis impar of Myxinoids as described by Müller, is I think insufficient, since we know nothing of its developmental history to enlighten us as to its origin and manner of growth, and the adult condition of the vessel cer-

tainly allows the inference that it is a reduced primitive dorsal aorta, — the exact homologue of the dorsal aorta of any vertebrate possessing the precardiac section.

In studying the course of the blood in the vessels of Chlamydoselachus, we find that the complete ellipse formed by each efferent branchial artery in the majority of Elasmobranch* species is wanting, and a single trunk collects the blood from all the gill leaflets borne by an arch, and consequently from one side only of any given gill sack. This is the primitive condition, and from Dohrn's researches we know that it is entirely in agreement with the embryonic structure of most of the Teleost and Elasmobranch embryos studied. It also agrees with the adult condition of Amphioxus. Parker very justly takes exceptions to the current use of the term "branchial vein," as applied to an efferent branchial vessel, and I quite agree with him when he says respecting the nature of these arteries (*loc. cit.*, p. 688): "These vessels are usually, but very incorrectly, called *branchial veins*. It would be quite as justifiable to speak of the *portal artery* as to call these obviously arterial vessels veins; a capillary system may be interposed in the course of an artery or of a vein, but this does not make the efferent trunk in the one case a vein, nor in the other the afferent trunk an artery." The collecting trunk is continued uninterruptedly to the dorsal aorta, so that an epibranchial artery in Parker's sense is not present in Chlamydoselachus. He says (*loc. cit.*, p. 689): "From the dorsal end of each arterial loop an epibranchial artery is continued backwards and inwards (Fig. 11); by uniting with one another successively in pairs these four trunks form the dorsal aorta. . . . In the embryo the aortic arches are continued directly from the ventral to the dorsal aorta. In the Holocephali and Teleostei there is only one efferent artery to each gill, corresponding to the anterior of the two efferent arteries in the Plagiostome holobranch. This is very evident in Callorhynchus, in which the single efferent artery of each gill is always cephalad of the corresponding afferent trunk. These facts tend to confirm the opinion to which one is led by the simple inspection of the parts in the adult Mustelus (compare *loc. cit.*, Figs. 6 and 17); namely, that the anterior efferent artery of each holobranch is to be looked upon as its primary revehent trunk and as strictly continuous with the corresponding epibranchial artery, the posterior efferent artery being a secondary vessel which debouches not into the primary trunk of its own, but into that of the next following gill." Such are Parker's conclusions from the study

* Cf. Hyrtl, *loc. cit.*, p. 4, and Parker (4) and (7).

of the anatomy of an adult Mustelus. As a result of his studies of the embryological history of the efferent arteries in Pristiurus, Dohrn[24] (page 3) establishes Parker's conclusions in a very complete and interesting manner.

Goette's account of the relations of the developing carotids in the embryos of Bombinator is as follows: "Bevor jedoch die Aorta vollständig angelegt ist, entwickelt sich eine neue besondere Verbindungsbahn zwischen den ersten Aortenbogen und der Aortenwurzel. Die Carotis hat sich nämlich schon während der Entwickelung des zweiten Aortenbogens bis an das Wurzelstück des ersten Wirbelbogens verlängert, unter welchem sie in die Sattelgrube eintritt, um von dort aus sich in zwei Aeste fortzusetzen. Der vorderen verläuft als ihre gerade Fortsetzung jederseits an der anatomischen Hirnbasis nach vorn wobei er durch das Austrittsloch des Sehnerven eine A. ophthalmica abgibt; der andere Ast (R. communicans carotidis posterior) steigt aus der Sattelgrube gerade auf und umgreift dem Vorderhirn dicht anliegend, dessen Basaltheil oder den Hirntrichter bis an seine Oberseite, wo er in dem sogenannten mittleren Schädelbalken Rathke's eingebettet ist. Von dort aus geht unser R. communicans in die Basalarterie seine Seite über, welche alsdann auch eine hintere Fortsetzung im Rückenmarkskanal besitzt sowie diese ihre Fortsetzungen unter dem Hirn und Rückenmark allmählich zusammenrücken, und sich endlich zum unpaaren medianer Stämme vereinigen, erscheint dieser als Zusammenfluss jener nach hinten konvergirendere Karotidenzweige. Die beiden primitiven Wirbelarterien und ihre noch getrennten vorderen Fortsetzungen, die Basalarterien, bilden also jederseits die hintere Hälfte, die inneren Karotiden mit ihren hinteren Verbindungszweigen die vordere Hälfte eines cerebralen Gefässbogens welche dem extracraniellen Herz-Aortenbogen gleichsam von oben aufgesetzt ist . . . so hört es bald noch zu ende der ersten Larvenperiode ganz auf, indem die primitiven Wirbelarterien verschwinden und ihrer Gebiet ganz den Carotiden überlassen (Taf. XXI. Fig. 377)."

The mandibular gill remains in a rudimentary condition, called in the Elasmobranch group spiracular gill or pseudobranch; in the Teleosts, on the other hand, the choroid gland (Balfour,[25] Müller[6]). It is not always present in Teleosts, according to the latter authority, but where it is developed its branches supply the choroid plexus of the eye. The artery of

[24] Dohrn, A. Die Entwicklung und Differenzirung der Kiemenbogen der Selachier. Mitt. Zool. Stat. in Neapel., V., 1884.

[25] Balfour, F. M. Comparative Embryology, II. p. 261.

Embryo of existing Elasmobranch.	Ancestral Form.	(Notidanidæ ?) Chlamydoselachus.	Mustelus (after Parker).
1st aortic arch.	A. branchialis $x + 1$.	Two lateral branches from the aorta into pituitary space.	
2d aortic arch.	A. branchialis $x + 2$.	The continuations of the internal carotid into pituitary space.	
3d aortic arch.	A. branchialis $x + 3$.	The anastomotic branch from the common carotid to the dorsal aorta = *mandibular* eff. br.	Commissure *w* (?) anterior carotid artery + pseudobranchial artery = mandibular efferent branchial arteries.
4th aortic arch. Hyoidean.	A. branchialis $x + 4$.	The *hyoidean* efferent branchial artery.	Vessel *y*; posterior carotid artery from origin to $x + 1$st afferent and 1st efferent branchial arteries.
5th aortic arch. 1st branchial.	A. branchialis $x + 5$.	1st branchial (efferent) artery.	1st epibranchial artery + 2d afferent, and 2d and 3d efferent arteries.
6th aortic arch. 2d branchial.	A. branchialis $x + 6$.	2d efferent branchial artery.	2d epibranchial artery + 3d afferent, and 4th and 5th efferent branchial arteries.
7th aortic arch. 3d branchial.	A. branchialis $x + 7$.	3d efferent branchial artery.	3d epibranchial artery + 4th afferent, and 6th and 7th efferent branchial arteries.
8th aortic arch. 4th branchial.	A. branchialis $x + 8$.	4th efferent branchial artery.	4th epibranchial artery + 5th afferent, and 8th and 9th efferent branchial arteries.
9th aortic arch. 5th branchial.	A. branchialis $x + 9$.	5th efferent branchial artery.	

the choroid gland comes from the hyoidean demibranch (Nebenkieme). The gland usually lies within the bony orbit, and with very few exceptions it is present in those species possessing a pseudobranch (i. e. in this case of course the hyoidean demibranch or its rudiment). The mandibular pseudobranch of Elasmobranchs and Ganoids lies behind the orbital territory, but there are cases in which an evident approach to the orbit is recognizable. The vessels of the mandibular pseudobranch consist of an afferent and an efferent artery, as in the perfect branchiæ, but usually they are shifted in position, so as to run more or less parallel to the long axis of the body, instead of transverse, as in the normal condition. The afferent trunk leaves the hyoidean efferent branchial just before the latter leaves the arch and passes forwards to end in the rete mirabile of the spiracular gill, while the efferent trunk arising from the rete passes forwards and inwards across the hind portion of the orbit into the cranial cavity, where it unites with the dorsal aorta by an anastomosis with the internal carotid, near the origin of the ophthalmic artery. The homology of the mandibular artery of Callorhynchus, as given by Parker, involves a mistaken identity, as we readily perceive by referring to the author's own works on the Skate and *Mustelus antarcticus*, as well as by reference to figures by Hyrtl (3) and Müller (6). It seems to me clear that the vessel designated *posterior carotid* by Parker is the arteria vertebralis.

It is of course possible that the arteriæ vertebrales of the Skate are a pair of musculo-spinal branches of a now vanished dorsal aorta, but from their prominent connection with the first efferent branchials of the Skate it is more probable that they are reduced efferent branchials — of the mandibular gill? The relations of the afferent and efferent vessels to the spiracular gill in Chlamydoselachus — a few leaflets of which still persist — I have not worked out satisfactorily as yet.

There are traces of other lateral branches to be found in the cartilage at either side of the aorta, between the occiput and pituitary prominence. In two sections I saw lateral unpaired vessels passing out from the median line to fade out in the cartilaginous tissue which appeared to be the cause of their suppression. Heptabranchias shows similar vessels. (See Figure 9.) They are so short and indistinct that it is with difficulty they can be traced without entirely destroying the cartilaginous floor of the skull in shaving it down thin enough to see them. The microscopic sections prepared from one of these transsections showed only a fibrous cord entirely destitute of a cavity. Presumably then the vessels were functional only during embryonic life. There is

a bare possibility that these vessels may have been the musculo-spinal branches of the segments taken into the cranium.

To the characters which Garman has selected as of value in properly placing Chlamydoselachus in the zoölogical system may be added : —

1. The dorsal aorta persistent throughout the entire length of the chorda, its precardiac portion of large size to the occipito-atlantal line, where it is suddenly much reduced to enter the cartilaginous basis cranii, through which it runs below and nearly parallel with the chorda, until it reaches the pituitary region, when it rises abruptly and becomes in part suprachordal, ending in a vascular plexus.

2. The absence of a complete vascular loop surrounding each gill slit, ending above in two efferent branchial arteries. Chlamydoselachus has but a single efferent branchial, placed in each instance cephalad of the corresponding afferent vessel, agreeing in this with the usual type of structure found in embryos of other Elasmobranchs.

There are several other characters belonging to other portions of the vascular system, of equal importance with the foregoing, indicative of simple organization, which we may take up at some subsequent date.

The character supposed by Müller to be diagnostic of the Cyclostomes, namely, that the dorsal aorta was continued beyond the union of the first pair of persisting efferent branchial arteries, and that it was still further connected with the anterior portion of the cephalic circle (in Myxine), is not alone peculiar to this group of fishes, but is also found among several Elasmobranchs. It still remains to be seen whether it is absent in all the bony fishes (including the Ganoids). If so, it would serve to show that the Cyclostomes and lower Elasmobranchs have retained their vascular apparatus in a much more primitive condition than the remaining groups. Müller did not find any trace of the precardiac aorta in Sturio, and from his description of the efferent branchial system it is extremely improbable that it exists in any form.

P. S. — The substance of this paper was written out in nearly its present form in the fall and winter of 1887, at which time the dissections were made, but circumstances have delayed the publication till this date.

August 1, 1889.

EXPLANATION OF FIGURES.

REFERENCE LETTERS.

a. artery (in Fig. 2, also auricle).
a. c. arcus cephalicus.
a. i. anterior innominate artery.
an. anastomotic branch of first efferent branchial artery.
a. pl. artery connecting pituitary plexus with hypophysis plexus.
b. a. bulbus arteriosus.
br. brachial vein.
c. cranial aorta (in Fig. 7, the cavity of this vessel).
c. a. conus arteriosus.
c. c. anterior carotid commissure (art. com. ant. D. S.).
cent. vertebral centrum.
ch. chorda dorsalis.
cœ. mes. cœliaco-mesenteric artery.
cor. coronary artery (+ hypobranchial trunk).
c. p. art. profunda cerebri.
c. p. a. posterior carotid commissure (art. com. post. D. S.)
c. c. cardinal sinus.
c. sh. chorda sheath.
ct. cartilage of the basis cranii, *c′*, *c″*, *c‴*, three layers of basis cranii.
ct. sh. cartilaginous sheath of chorda and cranial artery.
c. v. cardinal vein.
d. dorsal aorta (posterior to *k*).
d. m. dura mater.
e. c. external carotid artery.
e. ex. elastica externa of notochord.
g. median groove in ventral surface of basis cranii.
H. Hyoid arch.
h. v. hepatic vein.
hy. hypophysis.
i. c. internal carotid artery.
i. c. f. internal carotid foramen.
i. j. v. inferior jugular vein.
k. cephalic aorta. Kopfaorta, arteria spinalis impar Hyrtl, arteria vertebralis impar Müller.
kl. calcareous incrustation.

m. muscle.
me. membraneous wall overarching *c* near its anterior end.
m. s. arteriæ musculo-spinales.
ms. arteriæ musculo-spinales of the head.
n. nasal artery.
n. p. neural process.
o. ophthalmic artery.
p. palatine artery (= maxillary of Parker).
p. c. e. art. post. cerebri ext. D. S.
p. c. i. art. post. cerebri int. D. S.
p. c. s. precaval sinus.
p. pl. pituitary plexus.
pt. pituitary space.
r. c. subdural rete mirabile.
r. c. v. right cardinal vein.
r. p. rete mirabile profunda cereori D. S.
s. cl. subclavian artery.
s. j. v. superior jugular vein.
sp. anastomosing branch to spiracle.
s. v. sinus venosus.
tr. tropeic vein = lateral abdominal vein.
tr. b. fibrous trabeculæ crossing the channel of *c''*.
tr. c. transverse canal of pituitary region.
tr. p. transverse process.
v. ventricle.
v. a. ventral aorta.
vasc. vascular layer.

I.–IX. First to ninth pairs of aortic roots (arches).
1–6. First to sixth pairs efferent branchial vessels.
1′–6′. First to sixth pairs afferent branchial vessels.
1″–5″. First to fifth visceral arches.

Fig. 1. A sketch of a dissection of the efferent branchial vessels and the resulting aorta of *Chlamydoselachus anguineus*, natural size. On the right of the figure the vessels are sketched in the outline of the roof of the mouth, to the point of emergence from the tissue surrounding the proximal ends of the gill arches indicated on the left oval outlines. The left internal carotid artery is not shaded, and is sketched for a short distance only to show its course in the chiasm, at which point the cephalic aorta is broken for the sake of clearness. The end of the cranial aorta, and its branches connecting it with the pituitary plexus, are drawn somewhat enlarged.

Fig. 2. A semidiagrammatic figure of a portion of the vascular system of the same fish, showing the relations of the arterial and venous vessels, as seen from the left side. Approximately natural size. At * the coronary artery is cut off, nor are many of its branches shown. The venous vessels, heart, and ventral aorta are left unshaded. The common and internal carotids have been displaced upwards, and the anastomotic branch broken for sake of clearness.

Fig. 3. A sketch of the left half of the hemisected cranium of Chlamydoselachus to show the relations of the notochord and cranial aorta to the basis cranii and to the pituitary prominence and space. Natural size.

Fig. 4. (*a*) A view of the inner surface of floor of the cerebral cavity in the pituitary region before the removal of the dura mater and tissue which separates the brain cavity from the pituitary excavation and its contents (pituitary plexus, transverse canal, and carotid chiasm). Natural size. (*b*) A dissection of the ventral surface of the same, to show the chiasm of the internal carotids.

Fig. 5. A series of seven transsections of the basis cranii to show the relations of the notochord, cranial aorta, and the median ventral groove to each other and to the cranial floor.

Figs. 5*a* and 5*b* from **1** shown in Fig. 1. Figs. 5*c* and 5*d* from **2**; Fig. 5*e* from **3**; Figs. 5*f* and 5*g* from the pituitary prominence. All the figures enlarged. The series progresses cephalad, and the geometrical outlines refer to portions of the median line of Fig. 1.

Fig. 6. Part of the section of the notochord figured in 5*a* more highly magnified to show the sheaths and external calcified layer. × circa 180 diameters.

Fig. 7. A section of the cranial aorta from Fig. 5 *d*, more highly magnified. The fibrous trabeculae cross the cavity of the vessel in all directions. × 180 diameters.

Fig. 8. A transsection of the basis cranii of Chlamydoselachus, near the vertebral articulation, to show the figure made by the calcareous sheath (and its processes) of the notochord, resembling a vertebra of the trunk region.

Fig. 9. A transversely cut piece from the basis cranii of Heptabranchias sp. near the anterior third of the distance between the pituitary prominence and the occipital region, to show the chorda (and aorta ?) and the blood-vessels enclosed in the cartilage.

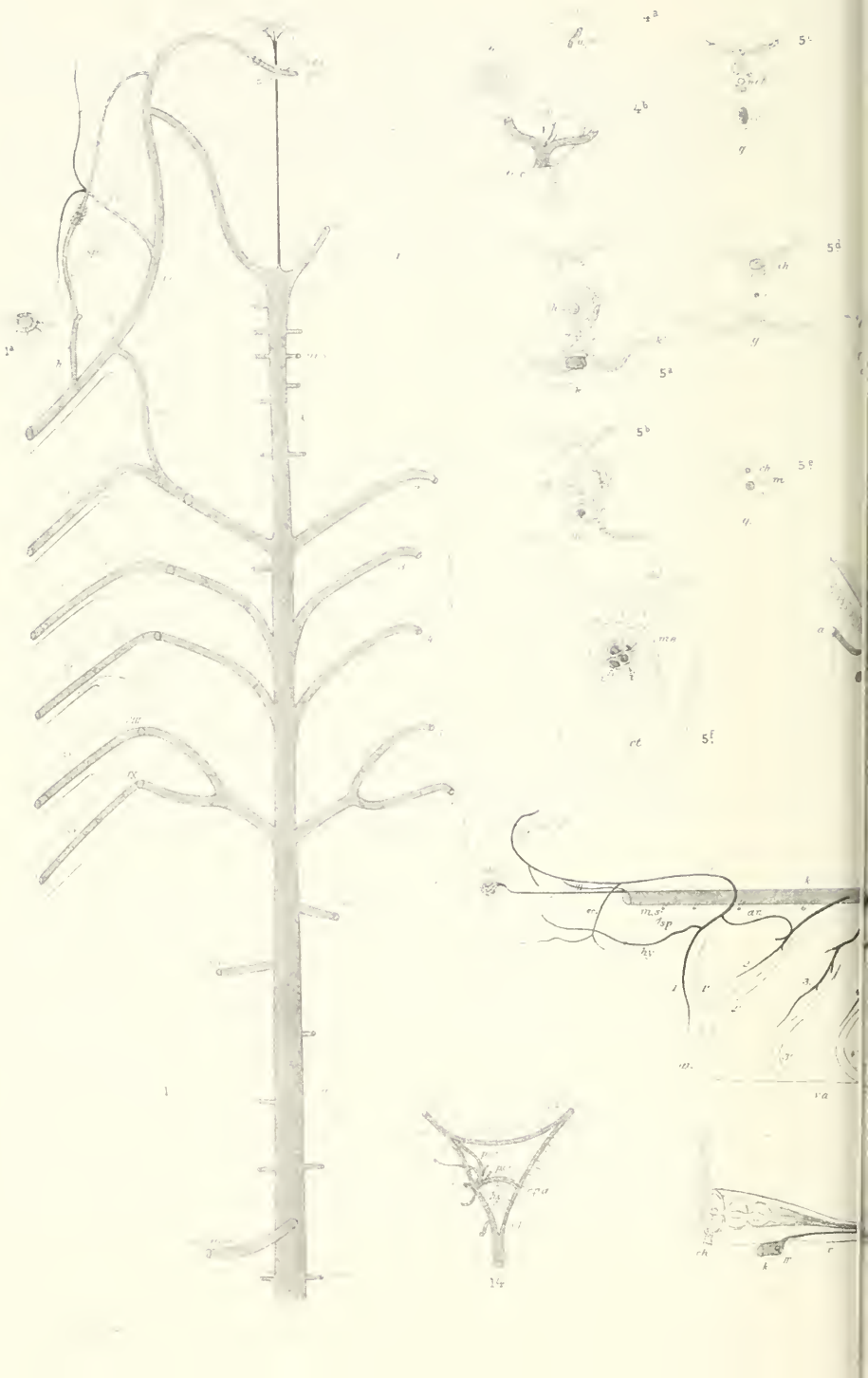
Fig. 10. The efferent branchial system and aorta of *Zygæna malleus*, after Hyrtl.

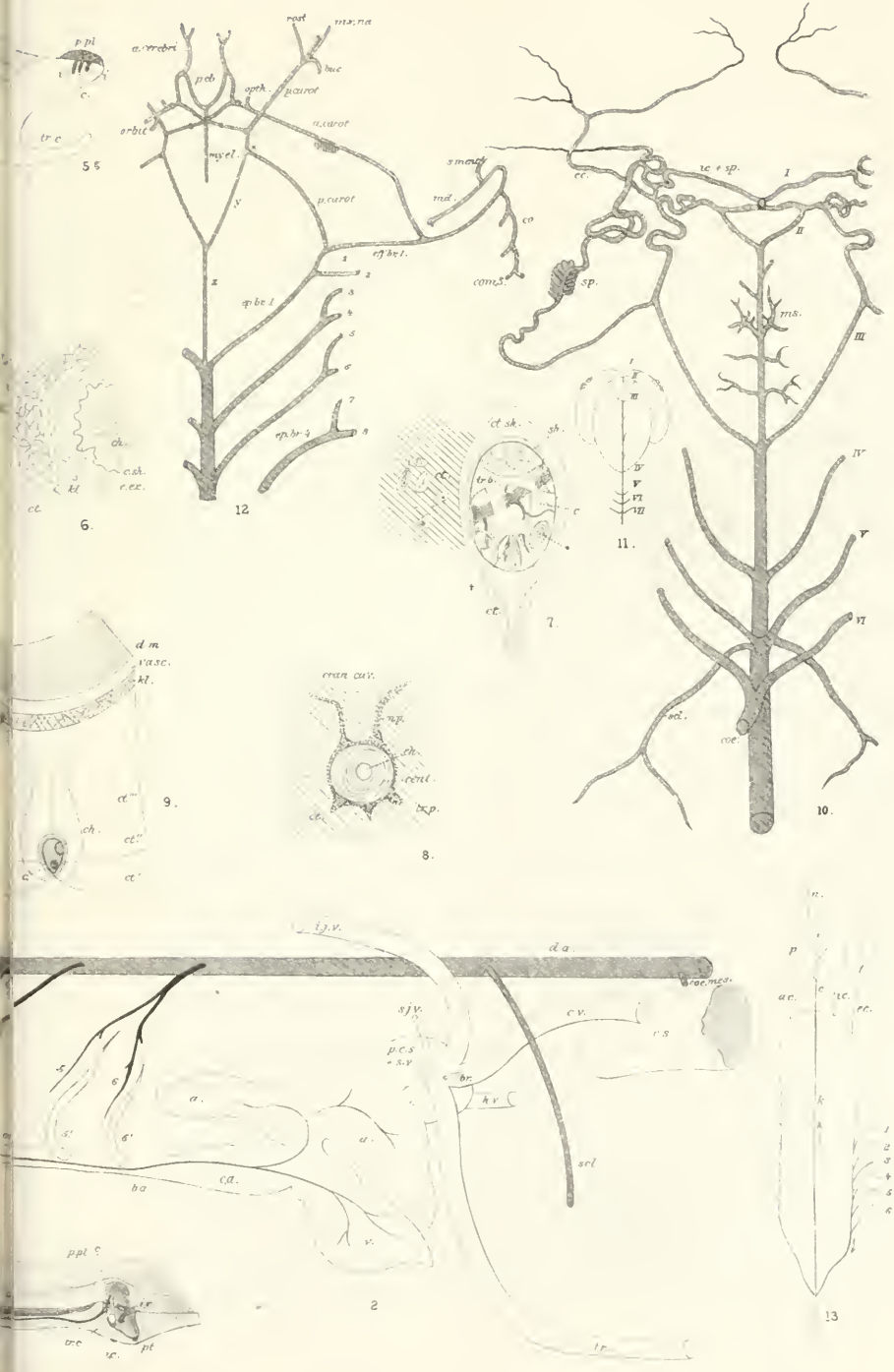
Fig. 11. Diagram of the above, with the "cranial aorta" inserted.

Fig. 12. The efferent branchial system of *Mustelus antarcticus*, after Parker.

Fig. 13. The efferent branchial system of Myxine, after Müller.

Fig. 14. The cephalic circle of Cephaloptera modified after De Sanctis.

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No. 6. — *Cave Animals from Southwestern Missouri.* By SAMUEL GARMAN.

THOUGH a knowledge of their inhabitants would appear to be of the greatest importance in connection with the study of the cave life of Kentucky, Tennessee, Indiana, and elsewhere, up to the present time the caverns of Missouri have received little or no attention from the zoölogist. The existence of numerous and extensive caves west of the Mississippi has been well known to geologists for a long time. There is frequent mention of them in the various Geological Reports; but among the notices only a single one touches on their animal occupants. The cavernous belt of Missouri is a hundred and fifty miles or more in width, and extends diagonally quite across the State from northeast to southwest. On the Mississippi, roughly estimated, it reaches from Clark to St. Louis County, and at the opposite extremity it stretches at the least from Vernon to Howell County. The geological positions of the caves range from the St. Louis limestone of the Lower Carboniferous to the third Magnesian limestone of the Lower Silurian. To the northward the formations lie in a plane that nearly coincides with that of the horizon. In Clark County the Keokuk limestone is at the surface; in St. Louis, it is that known by the name St. Louis; and between these points it is mainly the Burlington group that appears at the top. In the southwest a section across the belt cuts from the Carboniferous to the Silurian, as if toward a centre of upheaval in the southeastern portion of the State.

Caves have been reported from some twenty different counties, and in a number of instances particular ones have been described at length. Among the better known are those of Ralls, Boone, Phelps, Greene, Christian, Ozark, and McDonald. Whatever the causes, whether differences in the strata, the inclinations, the amount of fall in the watercourses, or in the water itself, the caves appear to become more extensive and more numerous toward the southwestern portion of the State. Fisher's Cave, in Ralls County, has an opening of ninety feet in width by twenty in height, and more than four hundred feet from the entrance

it connects with the surface by means of a sink-hole. The statement is made that Conner's Cave, in Boone County, has been explored for a distance of eight miles. Friede's Cave, in Phelps County, according to report, has been traced for a number of miles. There are several large caves in Ozark County, in the third Magnesian limestone. The sink-holes, with which so many of the caverns are connected, prove the manner of forming to have been the same as that giving rise to the Mammoth and other caves of Kentucky; the rock, dissolved and disintegrated, has been gradually removed by the water from the sink-holes. There seems to be no reason to suppose the history of the majority of these caves goes further back than that of the later Tertiary deposits, if so far. Such a small amount of divergence as exists between the species peculiar to the caves and their allies outside is proof that the former have entered their subterranean dwellings at a comparatively recent period.

In one of his Reports, State Geologist Broadhead remarks that in Christian County there is a stream that disappears in a sink to come out again three quarters of a mile away by an opening ninety-eight feet wide by sixty feet high, from which "a very clear, cool stream passes out, in which by careful search crawfish without eyes can be found." This is the only notice our search has revealed of the animals inhabiting these caves.

An opportunity of adding something to our knowledge was recently afforded by the kindness of Miss Ruth Hoppin, of Jasper County. My attention was first directed to the matter by a note from her, accompanied by a specimen of *Typhlichthys subterraneus*, Gir., that had been taken from a well. She said that similar fishes had been taken from other wells in the neighborhood, and that the owners of the wells spoke of subterranean streams flowing through. Experience elsewhere satisfied me that there should be caves in the vicinity from which these streams escaped, and at once my correspondent was asked if she would kindly engage some one to explore any caves there might be near by, and also, if possible, to get more specimens from the wells. She took up the matter, engaged help, and, at great personal risk and inconvenience, herself made explorations of a number of the caves, which, as was suspected, were not at all rare in the district, the southern part of Jasper County. Numerous specimens of Batrachians, Fishes, Crustaceans, Molliusks, and Insects were collected and forwarded from time to time, among them several new to science. Abstracts from the letters accompanying them give a very fair idea of their surroundings.

In one letter Miss Hoppin says: —

"I took a boy with me and went to Wilson's Cave. The catch was not large, but I was much encouraged by what I learned while there. The cave is about fifty feet long, nearly as wide, oven-shaped, and high enough to stand erect except around the sides. The farmer had enlarged the entrance to use the place as a creamery. A small very clear stream flowed along the left side, having a width of two feet and a depth of three, with a temperature of +54° F. About ten feet from the entrance the light struck the stream in such a manner that we could see everything in the water without a lantern. The first things that caught the eye were a lot of white crayfish, a dozen in all, like those I took from the wells. It seemed as if I might take every one of them. But though blind, they have one or more of the other senses very keenly developed. I am very sure they, as well as the white fishes, have the tactile sense developed in an unusual degree. At the least touch upon the water they dart away. As the net cautiously follows, they escape adroitly, making no blunders as to the direction of the approaching enemy, and hide in crevices of the jutting rocks or in the muddy bottom of the stream. The mud was easily stirred so that nothing could be seen. These creatures, fish and crayfish, are only to be secured by patient waiting and skilful management. The people at the cave say the fish never bite, and cannot be taken with hook and line. The crayfish were all found near the entrance, where there is considerable light. Following the stream back to a dark recess, reached by crawling on the slippery rocks, the light of the lantern revealed a school of little white fishes, such as I secured from the wells. All were very small. I saw half a dozen or more, but secured only one. I concluded the crayfish liked the light. Perhaps they remain near the entrance because they find there a supply of food. We found a few snails floating about, but saw none in the dark pool where the fish were. Miss Wilson, who was with me, thinks the crayfish devour the others. She has never seen them together, and says the latter keep away from the former, though she had not noticed the crayfish catching or eating them. There was nothing to prevent the crayfish ascending the stream to where the others were.

"An insect, a 'water spider,' common outside, is found inside near the light. I did not find it back where the little fishes stayed. By crawling back under the rocks one could see where the stream issues from the crevice. The passage is too low and too small to be followed, as the water occupies almost the whole of the opening. Beyond it, I think, one would find the home of the fish. The low opening is arched over by solid limestone, and could hardly be enlarged artificially, as the main entrance has been. Several feet to the right of the stream, having no visible connection with it, is 'the lake,' about fifteen feet in diameter. It is now a muddy bed. In no place could I see an inch of clear water. Just at the centre it has most water. When the water is high, the lake is full of fishes. What becomes of them when the water is low? I am ashamed that I did not look into that mud a little more carefully. There

must be some connection with the creek, either directly or back through the rocks. The lake is the place to catch the fish in high water. It is accessible, if one does not count the 'gumbo,' which makes an almost impassable sticky covering over the entire floor of the cave. This 'gumbo' forms the banks of the stream. It is difficult to keep one's footing there. With all our care it was constantly falling into the stream, roiling the water and scaring the crayfish. There was a small, dark-colored salamander near them. I brought home only one small fish and four small crayfish, the largest about two inches long. But I am much encouraged, for I feel sure that in time we can get all you want, and I realize there is ever so much that I can learn."

Samples of the "gumbo," or red mud, of the floors of the caves were sent with the collection. Experiments with it proved its excessive fineness and stickiness. Stirred about in the water at a depth only of two and a half inches, it was more than three hours before it had settled so that objects could be distinguished on the bottom. Twenty-four hours later, a cloudy substance, an inch and a half in depth, seemed to hang over the bottom, and it was more than two days before it had completely settled.

Miss Hoppin's first work was done in August; in September she made further efforts. In answer to questions, she states that the wells from which specimens have been taken are about half a mile from Centre Creek, the water level in wells and creek being nearly the same. The wells were nine or ten in number, from five to eighty rods apart, from eleven to thirty feet in depth, deeper in the higher ground, and having a depth of water varying from two to four feet. In some wells the rock at the bottom had been excavated. The water is what is commonly called hard, i. e. impregnated with lime. After rains, some of the wells have softer water than others, and the water stands higher in these wells, indicating closer connection with surface drainage. All the wells soon regain the common level. They become low in times of drouth, but never dry out entirely, as is the case with a cave spring near by, about twelve feet above the level of the creek. The temperatures taken in the wells at low water ranged from +52° to 54° Fahrenheit. During a storm, in the well having the highest water the temperature rose to +57°. When the mercury stood at 90° to 95° in the shade outside, the temperature was only 54° in Wilson's cave.

"After several days of a cold wave, the night temperature of the outer air being 45° and the noon reading at 60° to 70° in the shade, I found the temperature of the water in the cave had gone down about two degrees. . . . The level of this cave is ten or more feet above the creek, and it is not affected

by the rains until several days after the creek has begun its rise. This statement is from the people at the cave, and was not verified by me.

"From one well thirteen blind crayfish were taken by means of a net formed of mosquito bar spread on the bottom. The specimens became entangled in it. From the same well a few snails were taken. The owner reports, that at various times, a year or more ago, the surface of the water would be covered with 'little white lice or something of the kind.' Minnows were put in, after which the lice disappeared. A blind fish was also put into this well, but nothing had been seen again either of it or the minnows. From each of the other wells one crayfish was taken; from one of the three, a few minute centipedes. Earlier in the season these centipedes had been so numerous as to render the water unfit for use; they seemed to be inhabitants of the well. Some minnows were put in, and the centipedes vanished. I heard of them too late to make a satisfactory collection. From the Armstrong well two small blind fish were taken, and one from the Adams well. From the latter some snails were secured, also some large centipedes, these latter under circumstances indicative of accidental presence. Reports come from the country for miles around where fish and crayfish are taken. One well, an Artesian, went dry when a neighbor dug another farther down the hill. It was then found that the first well opened at the side directly into a small cave. All of these wells are in limestone; only in this formation is good water to be obtained hereabout. The larger caves in this vicinity are under the limestone cliffs and hills that skirt Centre Creek. The wells are usually walled with stones that leave spaces, through which the fishes may pass. There are probably many small subterranean springs and streams, not one large underlying lake or stream, as popular belief has it.

"Day's Cave, from which a small collection is sent, opens under the cliffs. After much digging the mouth was enlarged so that a small boy squeezed through. Wilson's Cave is not large; it is spanned by one limestone, and floored with the sticky 'gumbo.' This mud is utterly without grit. It forms a crumbling bank on the approachable side of the stream, and the minute particles are seen through the very clear water to be suspended in a thin swaying cloud at the bottom of the water. This mud-cloud is so light as to form no obstacle to the movement of the creatures which find it a ready hiding-place. It renders a study of the animals at the bottom very difficult, the water is so easily roiled. It required great care to catch the specimens; the stirring of the water frightened them away to their hiding places on the bottom, or among the dark nooks and crevices of the jutting rocks of the opposite bank, their movements at the same time stirring up the mud so that nothing could be seen. In the farthest corner of the cave, where the water comes in, would seem to be the home of the fishes; here they were most numerous and most active. When the water is low, they are found only here, though the stream below is equally cold and deep. Apparently, they avoid the light.

"On my first visit, the water being low, no crayfish were seen in the dark nook, the place favored by the fish. After the storm which had flooded the caves, a few were found there. Though I watched for some time, I never saw them pursue the fishes, as they might easily have done, guided by the stir in the water. Both creatures are very sensitive to the slightest ripple. During high water, a pool, 'the lake,' is formed, a little way from the stream in another dark part of this cave. In low water the pool is cut off from the creek. I found both species in it, the fish in the darkest part, and saw no signs of enmity. Most of the crayfish were found in the lower part of the stream, in the twilight; the fishes could not be found without the lantern. At the time of the floods, the cave is full, and the water rushes out furiously. . . . Another proof that the crayfish are more fond of the light is seen in the shallower wells. That from which most were taken was more exposed to the sun. At noon, when the light was more favorable, we could see them swimming about. No fishes have been taken from this well. They were taken in the narrower more shaded wells, of which the deep ones on the hills report fishes only.

"As to the food of the fishes, I discovered nothing. The mud where they were was not so deep as farther down. An examination of it the length of the cave brought to light many snails; the shells of the living ones are whiter and more nearly transparent than the floating dead ones. The largest crayfish are of a dirty rusty color, and very bristly, in caves and in wells. One large one is very soft and very white; no doubt it is newly moulted.

"Both fish and crayfish were less numerous after the freshet, and apparently less active. The disturbance of the flood may have caused them to retreat into their hiding places, only the weaker being left behind, or some may have been swept away by the torrent. The sensitive creatures would soon die in the light and heat outside, where the water is full of frogs and eyed-crayfishes. . . . The specimens become opaque when they are put into alcohol; they are almost transparent when alive, so much so that the action of their internal organs can be observed. Repeated tests assured me the animals were blind, though very sensitive to the sunlight. They died soon after catching, even in water frequently changed.

"The insects of the collection were taken in the lower part of the stream, near the mouth of the cave. They are similar to, if not identical with, others found in all the spring streams of this vicinity. They are very lively on the surface of the water, constantly rippling it. I think the crayfish eat them, but have no positive proof. On my first visit, insects and crayfish were very numerous at this place. The latter were darting up towards the former. We thought we could detect a faint odor about the insects (water spiders) that might help to guide their enemies, but the vibration of the water would be sufficient.

"Two aquatic and two terrestrial salamanders taken in this cave are in the collection; they are not peculiar to the cave. Some nearly a foot long are in the creek outside."

Some time near the middle of October Miss Hoppin visited Wilson's cave again, after some cold weather; the water was four degrees colder, and no fishes were to be seen. A couple of weeks later, after a week of warm days, the water had taken on its summer temperature of 54°, but there was nothing to collect. The water at this time was so low that the connection with the water of the inner cavern was broken, the water in the stream being below the fissure from which it poured earlier in the season. It appeared as if the fishes could not get out into the cave till the water rose again. The opening into the inner cavern would admit a small dog. There were no insects on the walls. Something was heard that was supposed to be a bat, but it could not be found. The neighbors said that after the floods white crayfishes were frequently found out of the cave in the creek.

Various caves were visited, at a considerable distance apart; the collections were in the main made from the wells and the two caves mentioned. It is evident from the notes that the caves are numerous, and similar to those in the same formations in other States. It is also evident, from what is found in the stomachs of the fishes, that there is more to be done in the way of collecting. A few fossils from the walls were sent. Though not peculiar to it, all are forms common in the Keokuk limestones, which lie at or near the surface in this district, known as the lead region of Southwestern Missouri. The greatest altitude is rather more than eleven hundred feet above the sea level. At the point under consideration the drainage goes to the westward. The waters afterward go south in the Grand River, then southeast in the Arkansas, and reach the Mississippi a little below 34° north latitude, two hundred and fifty miles or more below the mouth of the Ohio. Directly eastward, a considerable distance, the water is carried toward the mouth of the Arkansas, near which it meets the Mississippi. Northeastward it is less than twenty miles to points from which the drainage is carried through the Osage River to the Missouri, the mouth of which is about a hundred and fifty miles above that of the Ohio. Whether approached by the way of the Arkansas or by that of the Missouri, the caves of Jasper County and the neighboring counties are pretty effectually isolated from the caves east of the Mississippi, — a fact not to be lost sight of in discussing the distribution of the animals.

The collections contain a large number of specimens pertaining to a rather small number of species. Of these the fishes and the crustacea claim most of our attention, being the only ones we can with safety call peculiar to the caverns. As their testimony concerning the acquisition

of the species by the caves appears to differ somewhat, it will be well to consider them separately. The following is the entire list of species : —

Geotriton longicauda, from Wilson's Cave.
Plethodon sp., larvæ, " "
Cambarus virilis Hagen, from the wells, Wilson's Cave, and streams.
C. setosus n. sp., from the wells, Wilson's Cave.
Asellus Hoppinæ n. sp., from Day's Cave, in mud under stones.
Physa heterostropha Say, from caves and wells.
Scolopocryptops sexspinosa, from wells.
Plathemis trimaculata DeGeer, from mouths of caves.
Hygrotrechus remigis Say, from near mouth of Wilson's Cave.
Dineutes assimilis Aubé, " " "
Agabus sp., from Day's Cave, under rocks.
Ceuthophilus Sloanii Pack, from the water in Wilson's Cave.

FISHES.

Typhlichthys subterraneus Girard, the only blind fish in the collection, is represented by a large number of examples, the majority of them taken from the wells, the balance from the caves, with the exception of a single one from the creek outside. Compared with specimens from Kentucky and Tennessee, they agree so exactly as to raise the question whether the species was not originated in one of the localities and thence distributed to the others. The opinion generally held is, that the cave species of Indiana, Kentucky, and Tennessee originated in their respective localities. It is no doubt true for some of them. The idea is well supported by the insects and crustacea, the species in one section being unlike those of the others. It may be urged that the respect in which the fishes differ from them is more apparent than real, since these crustacea and insects were derived from a number of distinct species, while in all probability the same species of fish entered the caves in each district, and, being under the same influences in each, suffered the same modification in each. Reduced to its lowest terms the question, so far as the fishes are concerned, is this : Were the blind fishes distributed to the scattered localities where now found before or after they became blind? In favor of independent origins at distant points, it can be said that a species, distributed over the valley, possessed of habits such as would lead it to place itself under the modifying conditions of the cave in one place, would be most likely led to do so in the others. On the other hand, we have the more hesitation in accepting the conclusion that one and the same species originated independently in two or more different

localities, from knowing that exact parallels in the development of animals in nature, if they exist, are excessively rare. If our caution prevents ready acceptance of two apparently exact evolutionary parallels as really coincident, we become much more sceptical when the number of parallels or coinciding lines is increased. There is no doubt that the representatives of *Typhlichthys subterraneus* in the various caves were derived from a single common ancestral species. The doubts concern only the probability of the existence of three or more lines of development, in as many different locations, starting from the same species and leading to such practical identity of result. Such identical results would demand substantially similar modifying elements, — darkness, temperature, food, enemies, etc., — and the same length of time subjected to their influence. The likelihood of the existence of so many like elements in distant regions is inversely to the number demanded, though one cannot say it is impossible. To accept the conclusion favoring independent developments of the same species would involve acceptance of the idea that the caves in each of the districts had been occupied for about the same period of time. This, of course, would not furnish us with any clue to the time of formation of the caves.

As an alternative, the opinion is here advanced that these blind fishes originated in a particular locality, and have been, and are being, distributed among the caves throughout the valley. We are in the habit of looking upon great rivers like the Ohio or Mississippi as impassable obstacles to passage from cave to cave, rather than as thoroughfares. In this we have certainly assumed too much. Various instances are on record of the discovery of blind fishes that have strayed into the open streams from their caverns. If there were means of determining the frequency of the occurrence of such instances, it would undoubtedly much exceed what we are now inclined to credit. Persons acquainted with the streams of the Mississippi basin will agree that their undermined banks provide series of recesses or caverns, extending from the rills at the sources of the tributaries to the Gulf. The currents do not prove insurmountable to multitudes of fishes, no better provided with locomotive organs than the blind fishes, passing up the streams every season. Swept from the caves by the torrents in the flooded mouths, the blind species would find itself protected at once from light or enemies by the turbid waters. The temperature of the water at such times is low, and, should the light penetrate so as to prove detrimental, retreats exist on every hand in the excavations of the banks or the mud of the bottom. What migrations these fishes may make in

winter we can only imagine. Hiding places are so numerous and extensive as to suggest the possibility of the evolution of blind forms without the caves. The great essential would be the disposition to avoid the light, opportunities existing everywhere; the surroundings then would bring the organization into harmony with their demands, sooner or later as the creature was more or less plastic and yielding; disuse of the sense of sight being followed by its loss and atrophy of its special organ. Development of sightless forms in the holes and burrows of the banks, or in the mud of the bottom of the river, would here follow a similar course to that gone through at great depths in lake or ocean.

Crooked streams are not so impassable as one might suppose, even to floating objects, insects, mollusks, etc. A twig or leaf dropped into the current on the inside of the upper arm of a horseshoe curve in a stream is carried near to the opposite shore before it leaves the bend, and, especially if favored by the wind, often is carried completely across. The passage is much easier to animals that swim, however feebly. Taking everything into the account, it does not appear to be at all necessary to credit *Typhlichthys subterraneus* from Kentucky, Tennessee, and Missouri with more than a single point of origin. The same may be said of *Amblyopsis spelæus* of Kentucky and Indiana, and of the blind crayfish of the same States.

In an article entitled "Life in the Wyandot Cave," Ann. Mag. Nat. Hist., Ser. 4, VIII., 1871, p. 368, Professor Cope makes this statement concerning *Amblyopsis*: "If these *Amblyopses* be not alarmed, they come to the surface to feed, and swim in full sight, like white aquatic ghosts. They are then easily taken by the hand or net, if perfect silence is preserved; for they are unconscious of the presence of an enemy, except through the medium of hearing. This sense, however, is evidently very acute; for at any noise they turn suddenly downward and hide beneath stones, etc. on the bottom." The statement is repeated in Amer. Nat., 1872, p. 409. Such a development of this sense, in recesses where we are accustomed to think any sounds other than those made by the rippling or dripping water are almost unknown, is not what one would have expected. Having this in mind, I wrote to Miss Hoppin asking her to make experiments on *Typhlichthys*, and to determine what she could in regard to hearing, feeding habits, etc. The quotations here given are from her replies.

"For about two weeks I have been watching a fish taken from a well. I gave him considerable water, changed once a day, and kept in an uninhabited place subject to as few changes of temperature as possible. He seems perfectly

healthy, and as lively as when first taken from the well. If not capable of long fasts, he must live on small organisms my eye cannot discern. He is hardly ever still, but moves around the sides of the vessel constantly, down and up, as if needing the air. He never swims through the body of the water away from the sides, unless disturbed. Passing the finger over the sides of the vessel under water, I find it slippery. I am careful not to disturb this slimy coating when the water is changed. . . . Numerous tests convince me that it is through the sense of touch, and not through hearing, that the fish is disturbed: I may scream, or strike metal bodies together over him as near as possible, yet he seems to take no notice whatever. If I strike the vessel so that the water is set in motion, he darts away from that side through the mass of the water, instead of around, in his usual way. If I stir the water, or touch the fish, no matter how lightly, his actions are the same."

From the stomach of one specimen the remains of an *Asellus* were taken; from that of another, a young *Cambarus;* from a third, fragments of an insect resembling *Ceuthophilus;* and from others, portions of a crustacean, of which we have several specimens from Day's Cave, with well developed eyes, resembling *Crangonyx*, and from appearance the main food dependence.

The total length of the largest fish is two inches and a quarter. The eggs in the ovaries, August to September, are large, but with no traces of embryos.

CRUSTACEA.

In part, at least, the problem of the origin of the cave crustacea is simplified by the fact that they are so distinct in various caves as to leave no doubt that they are descended from ancestors already of different species at the time of entering the subterranean habitations. The blind crayfish of the Missouri caves is very distinct from any previously known; it is described below under the name *Cambarus setosus.* The common species of the neighborhood, *C. virilis*, is also found to enter the underground retreats, but it is not, of the outside forms, the nearest ally of the blind form. The latter bears so much affinity to *C. Bartonii* as to suggest derivation from it. A somewhat parallel condition exists in the caves of Missouri and those of Kentucky. In these last, with the blind *C. pellucidus* we find *C. Bartonii*, the nearest ally of the blind crayfish of Missouri, *C. setosus;* and with the latter again, in the Missouri caves, is found an eyed species, *C. virilis*, more nearly allied to the blind one in the Mammoth Cave. The relationship existing between the species *C. setosus* and *C. Bartonii* is much closer than that between *C. pellucidus* and *C. virilis.* A distribution of *C. Bartonii* covering so large a portion of

the Upper Mississippi valley to some extent favors the idea of a derivation from it of *C. setosus*. The greater differences between *C. pellucidus* and all the known eyed species point toward a longer subjection of that form to the spelæan influences. For comparison we give diagrams of details of structure, antennal lamina, epistoma, and the two forms of the anterior pairs of abdominal appendages of several species. These are taken from the specimens and from the drawings. The degrees of affinity are well indicated by the shapes of the first pairs of abdominal legs. The slighter approach of *C. pellucidus* toward *C. virilis* is shown by Figures 12 to 14 of the former, as compared with Figures 8 to 10 of the latter; and the nearness of *C. setosus* to *C. Bartonii* is apparent in Figures 1 and 2 of the first, and 4 and 5 of the second. Figures 11 and 15 represent *C. hamulatus*, from the Tennessee caves, a form which stands between *C. setosus* and *C. pellucidus*, nearer the former. Distributing the mentioned species into the groups arranged by Professor Hagen, we shall have the aberrant form *C. pellucidus* in the first group, nearest to the second, in which *C. virilis* belongs; while *C. Bartonii*, *C. setosus*, and *C. hamulatus* fall into the third group. Such close affinities as exist between *C. Bartonii* and *C. setosus* do not permit their separation into different genera, and the retention of the latter in the genus *Cambarus* cannot but be followed by the disestablishment of the genus *Orconectes* and the return to the older genus of the two species heretofore included in the later. Very young specimens of *C. setosus* correspond better with the adults of *C. Bartonii;* their eyes are more prominent in these stages, and appear to lack but the pigment; the rostrum also is less acuminate, and its blunt lateral angles are present. The gonopods of the very small ones agree with those of form ii. of *C. Bartonii*, the adult shapes approaching those of form i. According to Miss Hoppin, the young of *C. setosus* when alive are not so white as the older ones.

"At first, I attributed it to greater transparency, but now I am sure the color is in the shell, not that the internal organs can be seen because of the transparent shell. They are not so dark, however, as the brook species [*C. virilis*] of the same size."

In similarity to the case of *Amblyopsis*, the presence of the same species of blind crayfish in the caves of Kentucky and those of Indiana is an indication of distribution from a single point of origin.

The crustacea were placed in the hands of Professor W. Faxon for identification. He has kindly furnished the descriptions of the new species, which are given as they come from his pen. I have added on

Plate II. a hasty sketch of an adult female of *Cambarus setosus*, one half larger than natural size, and another of a specimen of *Asellus Hoppinæ*, three times the size of the specimen. On Plate II. Fig. 1, the outer two joints of each leg of the hinder two pairs are bent under, so that they appear one third shorter. The remainder of the collection, the insects, mollusks, and the like, was examined by Professor H. Garman, to whom I am indebted for identifications and notes quoted below.

Cambarus setosus Faxon.

"Carapace granulate on the sides, with scattered hair-like setæ; cervical groove sinuate; a small lateral spine just behind the cervical groove; rostrum of moderate length, triangular, excavated, lateral margins convex, no lateral teeth (except in smaller specimens, which have a small, acute tooth on each side near the tip); post-orbital ridges slightly developed, without anterior spines; region behind the cervical groove relatively long; areola very narrow, punctate. Abdomen about the same length as the carapace, with scattered hairs; telson bispinose (occasionally trispinose) on each side. Anterior process of the epistoma broadly triangular, margins more or less notched or dentate. Eye-stalks and eyes rudimentary. Basal segments of antennules furnished with a sharp spine near the distal end. Antennæ longer than the body; scale very broad at the distal end, external border slightly convex, ending in a short, sharp spine. Third pair of maxillipeds bearded within. Chelipeds of moderate length; chelæ long, very hairy, toothed on the inner margin, granulate on the outer margin; fingers long, compressed, costate; carpus toothed on the inner face, granulate on the outer side; upper surface of merqs granulate, lower surface with two rows of sharp spines. Third pair of legs of the male hooked. First pair of abdominal appendages terminating in two recurved hooks (similar to those of *C. Bartonii*). Annulus ventralis of the female prominent, with a deep central fossa.

"Length of one of the largest specimens, $2\frac{1}{2}$ inches; carapace, $1\frac{1}{4}$ in.; from tip of rostrum to cervical groove, $\frac{11}{16}$ in.; chela, $1\frac{1}{16}$ in.; fingers, $\frac{11}{16}$ in."

From the wells come also two very small specimens with well developed eyes, probably *C. virilis* Hagen. They are too young to determine with certainty.

Asellus Hoppinæ Faxon.

"Anterior margin of head with a median concavity, from the bottom of which projects a rostral tooth; external angles rounded; the head widens posteriorly, so that the hind margin is nearly as broad as the anterior margin of the first thoracic segment; eyes of moderate size, oval. Thoracic segments subquadrate, lateral margins convex, giving to the body with the head and

abdomen an even, long oval outline. Abdomen suborbicular, slightly excavated on the margin at the base of the caudal stylets. Basal segment of antennule subspherical, second segment cylindrical, forming with the first a well marked peduncle; flagellum composed of six or seven segments; the tip of the antennule does not reach the distal end of the penultimate segment of the antennal peduncle. Peduncle of antenna composed of three short, followed by two long segments; flagellum long, reaching, when bent backward, as far as to the abdomen. Mandible furnished with a tri-articulate palpus. First pair of thoracic appendages of male provided with a thick claw; on the palmary border are two long teeth and a small blunted tubercle; dactylus armed with a blunt tooth or tubercle near the middle. Caudal stylets with two subcylindrical branches, the inner of which is somewhat longer than the outer. Color, slaty brown mottled with lighter yellowish spots.

"Length, without caudal stylets, $\frac{3}{8}$ inch; breadth, $\frac{3}{16}$ inch."

INSECTS, etc.

The following are Professor Garman's notes on the invertebrates sent him for examination.

"The invertebrates sent me for identification pertain to common species, for the most part aquatic, such as one would expect to find at the mouths of caves from which emerge streams of water. With the exception of a myriapod and a small grub, all have well developed eyes. One or two may be classed as shade-lovers, since in ordinary situations they commonly affect retreats from which direct sunlight is excluded. The myriapod is totally blind, but is not, so far as I know, an inhabitant of caves. It is one of a number of widely distributed species, which spend much of their time in moist earth. The absence of eyes in a dipterous larva of the lot has also no necessary relation to a life in caves, since larvæ probably identical with it as to species are frequently taken among rubbish in open ditches and rivulets. The value of the collection is therefore to be looked for in the direction of its remote bearing on the problem of the origin of cave life, — a problem which needs for its complete elucidation all details obtainable which may by any possibility throw light upon this subject.

"The single mollusk of the collection, represented by many specimens from Wilson's cave, is *Physa heterostropha* Say, a species which is extremely common in the weedy shallows of ponds, lakes, and streams of the Middle States. It does not ordinarily avoid light more than other small fresh-water snails, and had perhaps penetrated the cave in following up its food supply. The examples are quite typical of the species.

"A myriapod, *Scolopocryptops sexspinosa* Say, is represented by one specimen marked 'From Wells.' Though lacking ocelli, it can hardly be considered a cave species, inasmuch as it is found everywhere throughout the eastern

United States under wood and stones. Its occurrence in wells is of course accidental.

"Three dragon-flies, two males and one female, taken at the mouth of Wilson's Cave, represent the *Plathemis trimaculata* De Geer, a swift-flying, light-loving insect which is common about fresh water in most parts of the United States.

"Seven examples of *Hygrotrechus remigis* Say were collected in Wilson's Cave, probably at no great distance from the entrance. These bugs prefer shaded waters, and are commonly seen on the surface of pools under bridges and culverts. Their eyes are relatively large, and they probably do not voluntarily visit regions entirely destitute of light.

"From the mouth of Wilson's Cave are four examples of the common whirligig beetle, *Dineutes assimilis* Aubé, differing in no respect from examples collected in other localities on open water.

"A second beetle, also aquatic, is represented by one specimen labelled 'Day's Cave, under rocks and stones in the mud.' It is a fine black *Agabus*, probably *A. suturalis* Crotch, but without authentic examples of this species for comparison it is hardly safe to make this determination final. From the Californian *A. lugens* Le Conte, to which it bears a close general resemblance, it seems to differ chiefly in having the sides of the prothorax a little rounded, and in having the basal margin sinuate.

"The 'cricket' seems to be *Ceuthophilus Sloanii* Pack., of which its discoverer says in a recent paper: 'The species is at once known by the conspicuous pale dorsal band which extends from between the eyes to the fourth segment behind, dilating slightly on the front edge of segments 2 to 4; the brown portion has scattered pale dots on each side of the line,' etc. The specimens are labelled 'From the water in Wilson's Cave.'

"The remaining specimen is a fleshy, wrinkled dipterous larva, 7 mm. long and 3 mm. in diameter, which was taken from a well."

November 16, 1889.

LIST OF DIAGRAMS.

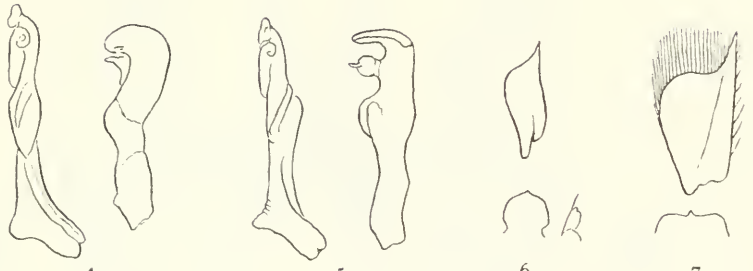
PLATE I.

Fig. 1–3, 7. *Cambarus setosus* Fax.
Fig. 4–6. *C. Bartonii* Fabr.; Gir.
Fig. 8–10. *C. virilis* Hagen.
Fig. 12–14. *C. pellucidus* Tellk.; Gir.
Fig. 11, 15. *C. hamulatus* Cope; Fax.

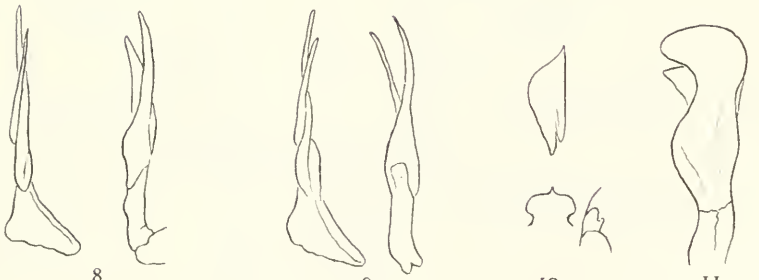
PLATE II.

Fig. 1. *Cambarus setosus*, 1½ times nat., ♀.
Fig. 2. *Asellus Hoppinæ*, 3 times nat.

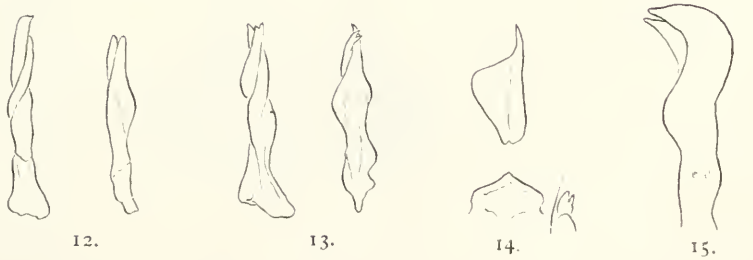
1. 2. 3.



4. 5. 6. 7.



8. 9. 10. 11.



12. 13. 14. 15.

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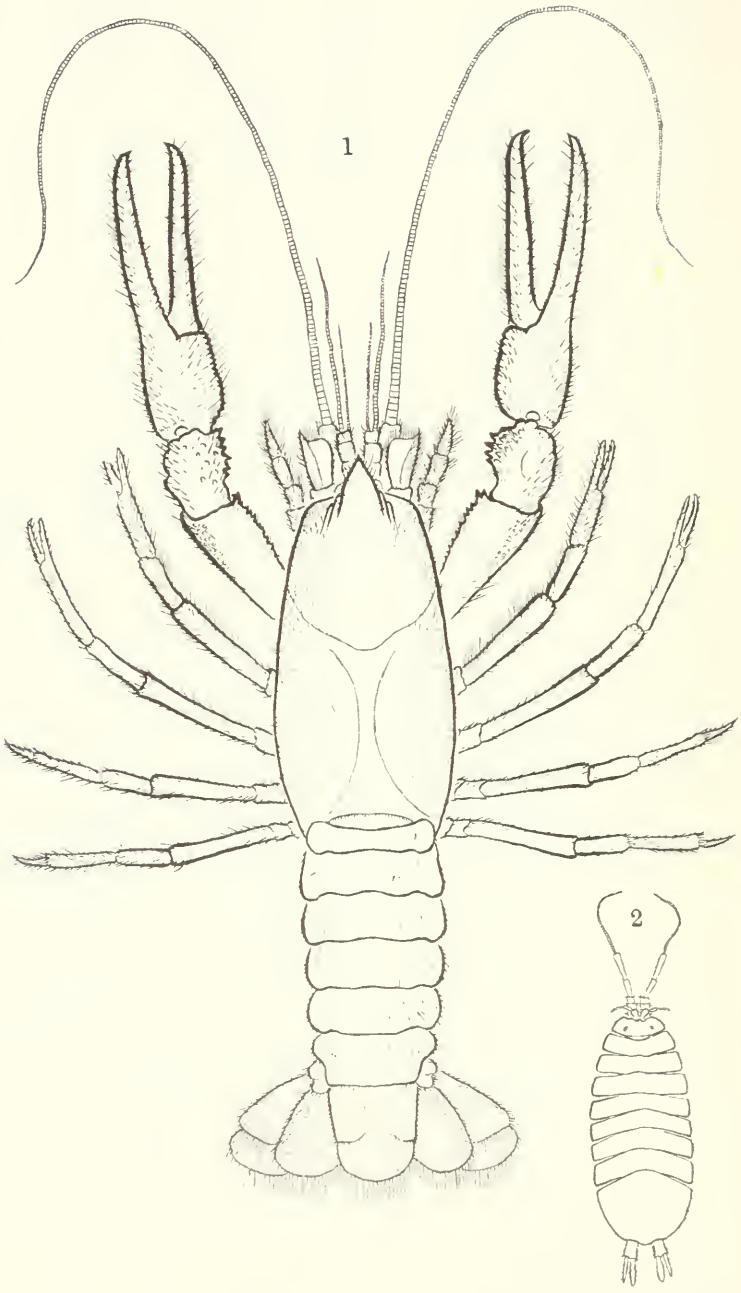

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